BULLETIN
OF THE RESEARCH COUNCIL
OF ISRAEL

Section D
BOTANY

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THE MAQUIS OF *QUERCUS CALLIPRINOS* IN ISRAEL AND JORDAN

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ABSTRACT

The *Quercus calliprinos–Pistacia palaestina* maquis association, one of the most characteristic plant communities of the East Mediterranean subregion, reaches its southern limit in Israel and Jordan mainly owing to the decrease in rainfall from North to South and from West to East. A subdivision of the East Mediterranean vegetation into eu-Mediterranean, oro-Mediterranean and sub-Mediterranean zones is proposed and illustrated by transects. The position of the *Quercus calliprinos–Pistacia palaestina* maquis within this zonal vegetation is discussed. It is a component of the *Quercetalia calliprini* order, and forms a part of the eu-Mediterranean zone. The association is subdivided into 3 subassociations: *galilaea, typica* and *depauperata,* each limited to a district of its own. In an analytical table the plants are grouped according to their phytosociological relations. The occurrence in this association of a considerable number of components of the *Poterietulia* order, *of* the *Varthemietea* and the *Rudereto–Secalinetea* classes and of the pioneers of the *Quercetea* class is discussed. The abundance of species in the association is a result of human interference. Also discussed are: stratification, life forms, phenoecology, root habits, regeneration, water relations, heat tolerance. The phytogeographical analysis of the association reveals that over 70 per cent of its components belong to the East Mediterranean element or to the East Mediterranean–Irano-Turanian group. Observations are recorded on the syngenesis of this association and on the recovery of the climax after destruction by man.

CONTENTS

Introduction. Climate and soils. The position of the *Quercus–Pistacia* maquis within the East Mediterranean zonal vegetation. The floristic composition of the *Quercus calliprinos–Pistacia palaestina* association. Distribution. Notes on the classification of the *Quercus calliprinos–Pistacia palaestina* association: *Subdivision of the association. The phytosociological relationships of the components.* Ecological remarks: *Stratification. Life forms and phenoecology. Root habits. Regeneration. Hydroecology. Thermoecology.* Floristics and phytogeography. Syngenesis: *The problem of the climax. Succession. Climax changes.* Man and maquis.

INTRODUCTION

The present article deals with the composition and ecology of the *Quercus calliprinos–Pistacia palaestina* association (Eig 1939, 1946), one of the most common and most characteristic plant communities of the Eastern Mediterranean. Together with a few other rather rare plant associations it forms the *Quercion calliprini* alliance, which is the most important part of the East Mediterranean zonal vegetation — the *Quercetalia calliprini* (Zohary 1955, 1960).

CLIMATE AND SOILS

Climate

The East Mediterranean maquis and forest vegetation reaches its southern limit in Israel and Jordan. From the latitude of Gaza in Southern Palestine westward to the environs of Derna in Cyrenaica, no arboreal Mediterranean plants occur. This Sinaitic-Lybian gap in the circum-Mediterranean vegetation belt is primarily the result of low amount of rainfall which throughout this gap is far below 300 mm.

North of the latitude of Gaza in Palestine and that of Petra in Transjordan, there extends a belt of maquis and forest climax vegetation up to the Lebanon range and further north to Syria and Western Anatolia.

The annual amount of rainfall decreases from 1200 mm (Lebanon, Amanus mountains, etc.) to 350 mm (Southern Israel and Jordan), and the maquis — especially the *Quercus-Pistacia* association—show corresponding variations in composition and density. In a West - East direction the decrease in rainfall is even more abrupt. The strongest gradients mark those parts where the eastern escarpments of the Mediterranean ranges are rather steep, as in the mountains of Amanus, Cassius, Lebanon, Galilee and Judaea. In the Jerusalem area, for instance, where the mean annual rainfall decreases from about 600 mm to 250 mm within 3 km East of the city, the arboreal Mediterranean vegetation abruptly disappears at the eastern outskirts of the city.

Temperature, too, controls the distribution of the oak-pistacia community and it is second only to rainfall. The fact that throughout the Eastern Mediterranean this maquis and forest association makes its appearance from about 200 m upwards* is apparently due to its demand for winter temperatures lower than those required by the maquis of *Ceratonia siliqua*, which occupies the lowermost zone of the mountains. The upper altitudinal limit of distribution of the *Quercus–Pistacia* community is less well defined. It becomes lower the further North we proceed. In Israel this community ascends to altitudes of 1,200 m (Har Meiron). Generally, it does not occur higher than at above 1,000 m, but in the Lebanon and in Jordan (Edom) stands of *Quercus calliprinos* have been observed also at a height of 1,500 m.

Table I shows rainfall and temperature data for a few typical localities of the oak maquis area in Israel.

Soils

Typically, the *Quercus–Pistacia* maquis grows on terra rossa. This soil type is derived from hard limestone and dolomites of the Upper Cretaceous as well as from certain

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* In the interior parts of Israel, where the *Ceratonieto–Pistacietum lentisci* does not form a lower maquis belt, the *Quercus–Pistacia palaestina* association may occasionally appear also at altitudes lower than 200 m.

Eocene rocks. This is an A-C soil in which the A-horizon, when under vegetation, consists of a humiferous subhorizon (Ao_1) which merges into the brown to dark-brown mineral subsoil (A_1). Destruction of the vegetation leads to a removal of the humiferous layer whereupon the soil turns red. In the region of the maquis the soil is everywhere fairly shallow and rocky outcrops are abundant, even under the canopy of trees. The plants of the maquis are well adapted to these conditions, primarily by being able to penetrate with their roots into the crevices of hard limestone and into deeper soil pouches. Terra rossa contains a fairly high amount, up to 35 per cent of $CaCO_3$. It is alkaline and comprises a rather high silt-clay fraction. The *Quercus-Pistacia* maquis also grows on rendzina — a highly calcareous soil derived mainly from soft Senonian and Tertiary rocks, as well as from the so-called "Nari" crusts. This soil has a very shallow profile and is grey to white - greyish in colour. It is less humiferous than terra rossa and is underlain by a continuous, rather soft parent rock. The differences in soil conditions are reflected in the considerably larger number of herbaceous components in terra rossa, where soil pouches are formed, as compared with rendzina. On the other hand, the wilting percentage is lower in rendzina than it is in terra rossa. On Mt. Carmel, the available moisture in terra rossa and rendzina soils was found to be 15.4 and 18.5 per cent respectively. This difference is particularly significant in summer and seems moreover to exert decisive influence on seedling establishment. Thus it was found that in summer, seedlings of *Pinus halepensis* survive on rendzina, whereas they succumb to the summer drought on terra rossa. The *Pistacia* maquis does not occur on basalt soils and on sand dunes or hydropedic soils.

THE POSITION OF THE *Quercus-Pistacia* MAQUIS WITHIN THE EAST MEDITERRANEAN ZONAL VEGETATION

The East Mediterranean zonal vegetation may be subdivided into three zones: (a) eu-Mediterranean, (b) oro-Mediterranean and (c) sub-Mediterranean. The eu-Mediterranean zone comprises thermophilous evergreen vegetation and includes the *Quercetalia calliprini* (maquis and forests) and the *Poterietalia spinosi* (dwarf shrub vegetation). The *Quercetalia* comprise the *Ceratonio-Pistacion* (Zohary and Orshan 1959), the *Quercion calliprini*, the *Pinion halepensis* and the *Quercion ithaburensis* (Zohary 1946, 1955, 1960). The eu-Mediterranean zone is limited in both longitude and altitude. In higher altitudes it is replaced by the oro-Mediterranean vegetation and towards the interior by a sub-Mediterranean (semi-steppe) belt. The vegetal composition of the oro-Mediterranean zone varies from North to South. It may be subdivided into a montane zone and a subalpine zone of arboreal vegetation. The montane zone is characterized by the *Quercetalia cerridis orientalia*. This order is well represented in the Lebanon, Amanus, Taurus, etc. As a rule, it occupies a belt between 800 and 1,500 m which partly overlaps with the eu-Mediterranean and partly with the subalpine zone. The subalpine zone comprises the *Cedretum libani*, *Abietum cilicicae*,

Juniperetum excelsae as well as *Fagetum orientalis*, etc., which demand more mesic conditions.

The sub-Mediterranean belt extends horizontally along the eastern fringes of the Mediterranean vegetation, bordering on steppes and deserts. It is less clear-cut than the altitudinal zones. Some associations, such as *Juniperetum excelsae*, *Quercetum pubescentis* (Turkey), the *Crataegus-Amygdalus* association or *Pistacietum atlanticae* (Syria, Palestine), may well characterize this zone, which is generally transitional between the Mediterranean and the Irano-Turanian territories.

The following transects, at four different latitudes within the East Mediterranean belt of maquis and forests, may illustrate the altitudinal differentiation of the vegetation.

Transect 1. Southern Israel: Mediterranean Coast — Judaean Desert (from Yad-Mordekhai, between Gaza and Ashkelon — to Amatsia, Hebron and Beni Naim). At this latitude there is no maquis in the Coastal Plain, including the "kurkar" hills and the alluvial plains. Judging from extant plants, it appears fairly certain that this area was occupied by a subtropical vegetation of the *Hyparrhenietea hirtae* class. Further to the East, the foothills are covered with the *Ceratonieto–Pistacietum lentisci* up to an altitude of about 300 m. In the environs of Amatsia (Duwaima), this association is gradually being replaced by the association of *Quercus calliprinos–Pistacia palaestina* which ascends up to the altitude of Hebron and disappears a few kilometres to the East of that town. Scattered trees and small stands of *Pistacia atlantica*, occurring in Hebron and East of the city, belong to the sub-Mediterranean belt adjacent to the Irano-Turanian territory. Because of the comparatively low altitude (not over 1,000 m), the area is not suitable for oro-Mediterranean vegetation.

Transect 2. Northern Israel: Mediterranean Coast – Hule Plain (from Nahariya, through Mt. Meiron to Mishmar Hayarden). The coastal dunes, the adjacent alluvial plain and the foothills up to 300 m above S. L. have as their climax the *Ceratonieto-Pistacietum lentisci*. Higher up, in the mountains of Galilee, the association of *Quercus calliprinos – Pistacia palaestina* becomes dominant, ascending up to the highest peaks (1,200 m). However, from somewhat below these peaks there penetrate into the evergreen association single components or fragments of a deciduous forest association (*Quercetum infectoriae*) of the oro-Mediterranean zone which is common in the Lebanon and Antilebanon. On the eastern escarpments of the Galilean mountains the oak association is replaced by a particular variant of the *Ceratonieto-Pistacietum* (Zohary and Orshan 1959) which, in turn, is fringed to the East by scattered trees and stands of *Quercus ithaburensis* and *Pistacia atlantica*.

Transect 3. Northern Lebanon: Mediterranean coast – Bak'a (from Tripoli to Hermel). On the rather steep Western slopes of the Lebanon, remnants of the *Ceratonieto-Pistacietum lentisci myrtetosum* occur up to 200–300 m above S. L.

Higher up, to about 1,000 m, remnants of the *Quercus calliprinos-Pistacia palaestina* association are dominant. As this community is largely destroyed, *Pinetum brutiae* replaces it in several localities, with many components of this oak association as underwood. In this transect, the *Pinetum* is particularly well developed in the 1,000–1,400 m belt. In the underwood, *Quercus calliprinos* may exceptionally occur even at that height. *Quercetum infectoriae* of the montane zone generally first appears at 800 m. Either as an independent association or as underwood in the *Pinetum brutiae* it extends up to 1,500 m. *Quercetum cerridis* mainly flourishes between 1,300 and 1,500 m, both as free stands and as underwood in the *Pinetum brutiae*. The occurrence of *Pinus brutia* in both the eu-Mediterranean zone (*Quercus–Pistacia* association) and the montane zone (*Quercetum cerridis, Quercetum infectoriae*) does not obliterate the altitudinal belting of the vegetation, as *P. brutia* is known to be extremely occupative wherever Mediterranean arboreal broad-leaved vegetation is being destroyed. At still higher altitudes in the subalpine zone the 1,400–1,800 m belt is characterized by the *Cedretum libani* and the *Abietum cilicicae*. The *Juniperetum excelsae* occurs between 1,300 and 2,000 m and is also occupative in this zone. The overlapping of individual vegetation zones is due to extensive human interference with the arboreal vegetation. Descending the eastern escarpments of the Lebanon, one again passes the *Quercus calliprinos-Pistacia palaestina* association (e.g. in the environs of Fnediq). Further down scattered trees of *Crataegus, Pyrus* and *Amygdalus* indicate a sub-Mediterranean vegetation belt which completes the zonal system towards East. Already at Hermel there is an Irano-Turanian steppe vegetation.

Transect 4. S. Turkey: Alexandretta to Kirkhan (Amanus Mountains). The lowest 100 m zone is occupied by the *Ceratonieto-Pistacietum lentisci myrtetosum*. Higher up, to 800 m, maquis of *Quercus calliprinos–Pistacia palaestina* is very well developed. *Pinetum brutiae* is found all along the slopes up to 1,200 m. The montane zone is covered by *Quercetum infectoriae* together with minor stands of *Quercetum cerridis*. With suitable exposure, both may occur already at an altitude of 600 m, thus partly overlapping with the evergreen oak maquis. Here, too, *Pinus brutia* readily occupies sites of destroyed or damaged forest and maquis and so occurs both in the zone of the evergreen maquis and in that of the deciduous forest. The leading plants of both the maquis and the forest may occur as underwood in this *Pinetum*. Above 1,300 m, *Pinetum nigrae* occupies a zone extending over 200–400 m of width. Between 1,900–2,100 m stands of *Cedrus libani, Abies cilicica* and *Fagus orientalis* were found. At the eastern outskirts of the mountains, remnants of the *Quercus–Pistacia* maquis recur. Further eastwards the latter is replaced by scattered trees of *Amygdalus, Pyrus, Crataegus*, etc.

The preceding transects clearly show the eu-Mediterranean character of the association under review, which is enclosed between the deciduous forest zone and the evergreen thermophilous zone of the *Ceratonia-Pistacia* community.

THE FLORISTIC COMPOSITION OF THE *Quercus calliprinos-Pistacia palaestina* ASSOCIATI

In Table II the plants of the 55 records have been arranged within the the vario plant sociological categories*. All records refer to quadrats of about 400 m². T category of characteristics includes, in addition to exclusive species, also preferenti regional and differential ones.

List of Low Presence Species**

Group I. Characteristics of the association: *Ferulago syriaca* Boiss. (4), *Aristolochia paecilan.* Boiss. (3), *Asperula libanotica* Boiss. (3), *Brachypodium pinnatum* (L.) R. et S. (3), *Vicia tet sperma* (L.) Schreb. (3), *Cephalanthera longifolia* (Huds.) Fritsch (2), *Dryopteris villarsii* (Be Woynar (2), *Scilla palaestina* Feinbr. (2), *Verbascum galilaeum* Boiss. (2), *Viburnum tinus* (2), *Aristolochia altissima* Desf. (1), *Carex distans* L. (1), *Delphinium ithaburense* Boiss. (*Galium hierosolymitanum* L. (1), *Knautia integrifolia* Bert. (1), *Lamium striatum* S. et S. (*Lapsana ramosissima* Boiss. et Heldr. (1), *Pimpinella peregrina* L. (1), *Silene picta* Pers. (*Symphytum palaestinum* Boiss. (1), *Veronica leiocarpa* Boiss. (1).

Group II.   Characteristics of the alliance and order: *Allium neapolitanum* Cyr. (3), *Euphor. thamnoides* Boiss. (3), *Verbascum tripolitanum* Boiss. (3), *Melissa officinalis* L. (2), *Oph. sintenisii* Fleisch. et Bornm. (2), *Orchis galilaeus* Schltr. (1), *Scaligeria hermonis* Post (*Smyrnium olusatrum* L. (1), *Thesium bergeri* Zucc. (1).

Group III. Characteristics of the *Poterietalia* order: *Linum corymbulosum* (Planch.) Rchb. (*Micromeria graeca* (L.) Bth. (4), *Pisum fulvum* S. et S. (4), *Teucrium polium* L. (4), *Torilis arven* (Huds.) Lk. (4), *Arrhenatherum palaestinum* Boiss. (3), *Cynosurus echinatus* L. (3), *Lactu. cretica* Desf. (3), *Scilla hyacinthoides* L. (3), *Tragopogon longirostre* Bisch. (3), *Valeriane. coronata* (Willd.) DC. (3) *Anthemis discoidea* (All.) Vahl (2), *Campanula sidoniensis* Boiss. Bl. (2), *Convolvulus pentapetaloides* L. (2), *Convolvulus scammonia* L. (2), *Geropogon glabr. L. (2), *Pimpinella cretica* Poir. (2), *Thrincia tuberosa* (L.) Lam. et DC. (2), *Thymus capita. (L.) Lk. et Hoffm. (2), *Valerianella truncata* (Rchb.) Betcke (2), *Artedia squamata* L. (1), *Ar. dioscoridis* S. et S. (1), *Arum palaestinum* Boiss. (1), *Bellis sylvestris* Cyr. (1), *Clypeola jonthla. L. (1), *Helianthemum lavandulaefolium* Mill. (1), *Inula viscosa* (L.) Desf. (1), *Ophrys fusca* Lk. (*Orchis papilionaceus* L. (1), *Polygala monspeliaca* L. (1), *Ricotia lunaria* (L.) DC. (1), *Sal. judaica* Boiss. (1), *Scutellaria peregrina* L. (1), *Silene behen* L. (1), *Teucrium creticum* L. (*Thymbra spicata* L. (1), *Trifolium boissieri* Guss. (1), *Trigonella berythaea* Boiss. et Bl. (1), *spinosa* L. (1), *Tulipa montana* Lindl. (1), *Valeriana dioscoridis* S. et S. (1), *Valerianella kotsc. Boiss. (1).

Group IV.   Characteristics of the *Ballotetalia* order: *Linaria aegyptiaca* (L.) Dumort., *Urgi. maritima* (L.) Bak. (2), *Chardinia orientalis* (L.) Ktze. (1), *Echinaria capitata* (L.) Desf. (1), *Iris sisyrhinchium* L. (1), *Scrophularia xanthoglossa* Boiss. (1), *Triticum dicoccoides* Koern. (*Ballota undulata* (Fresen.) Bth. (1).

Group VII.   Characteristics of the *Varthemietea* class: *Galium articulatum* (L.) R. et S. (*Vaillantia hispida* L. (3), *Campanula hierosolymitana* Boiss. (2), *Crepis hierosolymitana* Boiss. (*Cynocrambe prostrata* Gaertn. (2), *Parietaria lusitanica* L. (2), *Campanula aaronsohnii* Even. (1), *Ceratocapnos palaestina* Boiss. (1), *Ceterach officinarum* Lam. et DC. (1), *Cheilant. fragrans* (L.) Webb et Berth. (1), *Galium judaicum* Boiss. (1), *Trifolium scabrum* L. (1).

Location of Records

Records   1—4   Eastern Upper Galilee, Mt. Meiron.

           5   Central Upper Galilee, on the way from Peqi'in to Rama.

           6   Central Upper Galilee, on the way from Eilon to Saasa.

          7—9   Western Upper Galilee, Wadi Qarn, env. of Ras-en-Nabi.

         10—13   Western Upper Galilee, env. of Eilon, descent to Wadi Qarqara.

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* The species with low degrees of presence (less than 6%) have been listed separately.
** Figures in brackets indicate the number of records in which the species was present.

14—19   Western Upper Galilee, env. of Hanita.
20—24   Mt. Carmel, between Hreibe and Nesher.
25—26   Mt. Carmel, on the way from Hreibe to Yagur.
  27   Mt. Carmel, km 4 on the way from Beit Oren to Daliat-el-Carmel.
28—31   Mt. Carmel, env. of Muhraka.
  32   Mt. Carmel, env. of Yokneam.
33—38   Samaria Mts., Mt. Hetery.
39—42   Samaria Mts., Wadi Malik, opposite Shefeya.
43—51   Central Judaean Mts., between Bar-Giora and Eilah Plain.
52—54   Southern Judaean Mts., 10–16 km N. of Beit Govrin.
  55   Southern Judaean Mts., env. of Kefar Yeshaya.

DISTRIBUTION

The climax area of the *Quercus–Pistacia* association comprises the bulk of the Mediterranean territory in Palestine, from the mountains of Galilee to the southern limit of the Judaean Mountains. While there are still large stretches of this maquis in Galilee, Mt. Carmel, Samaria, Judaea and Gilead, a considerable proportion of the original climax area, owing to man's interference, is at present occupied by dwarf shrub communities of the *Poterietalia* order (Map 1).

The *Quercus calliprinos* stands in Edom (Transjordan) presumably form another association in which *Juniperus* and *Pistacia atlantica* are important components. As our data on this association are inadequate, we do not consider it here. Outside Palestine we met with this association in Lebanon, Syria, Turkey and South-Eastern Greece. From literature data it seems to occur in Cyprus, Crete and almost in all the Aegaean Islands.

ON THE CLASSIFICATION OF THE *Quercus calliprinos-Pistacia palaestina* ASSOCIATION

Subdivision of the Association

In the analytical table three subassociations have been distinguished: (1) *galilaea*, (2) *typica* and (3) *depauperata*.

Subassociation *galilaea* (Figure 1) comprises the oak maquis of Galilee. It is distinguished by its floristic richness, as well as by the fact that within this area numerous species occur, notably libanotic ones, which are not found elsewhere in Israel. Species so far known to belong to this group are *Acer syriacum, Prunus ursina, Gonocytisus pterocladus, Scilla palaestina, Dryopteris villarsii, Rubus tomentosus, Verbascum galilaeum, Paeonia corallina, Hedera helix, Sorbus trilobata* and many others. This subassociation is undoubtedly the most mesic type of the *Quercus–Pistacia* maquis. Two variants of this subassociation may be distinguished: (1) The Meiron variant, which includes some representatives of the deciduous *Quercetum infectoriae*
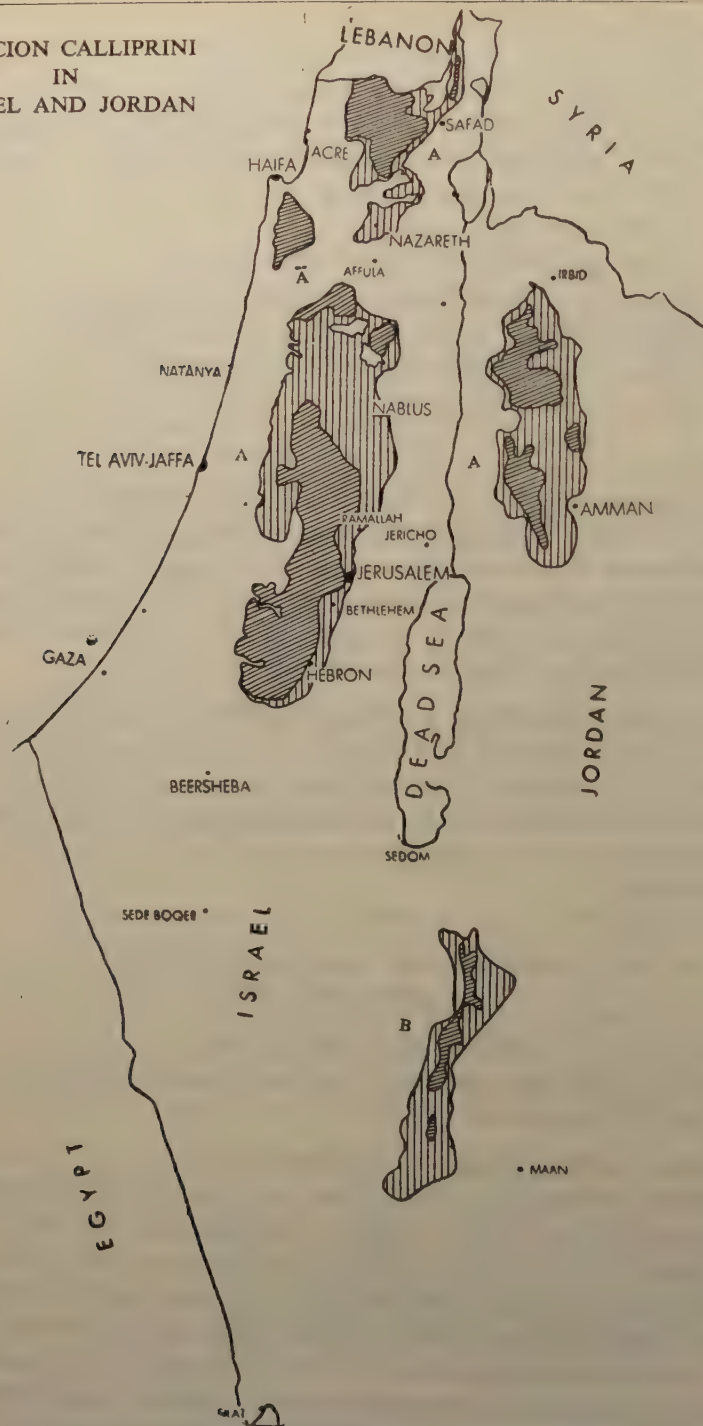
Map 1

A — Assoc. of *Quercus calliprinos* — *Pistacia palaestina*. B — Assoc. of *Quercus calliprinos* — *Juniperus phoenicea*. Vertical lines: climax area; diagonal lines: actual stands.

Figure 1

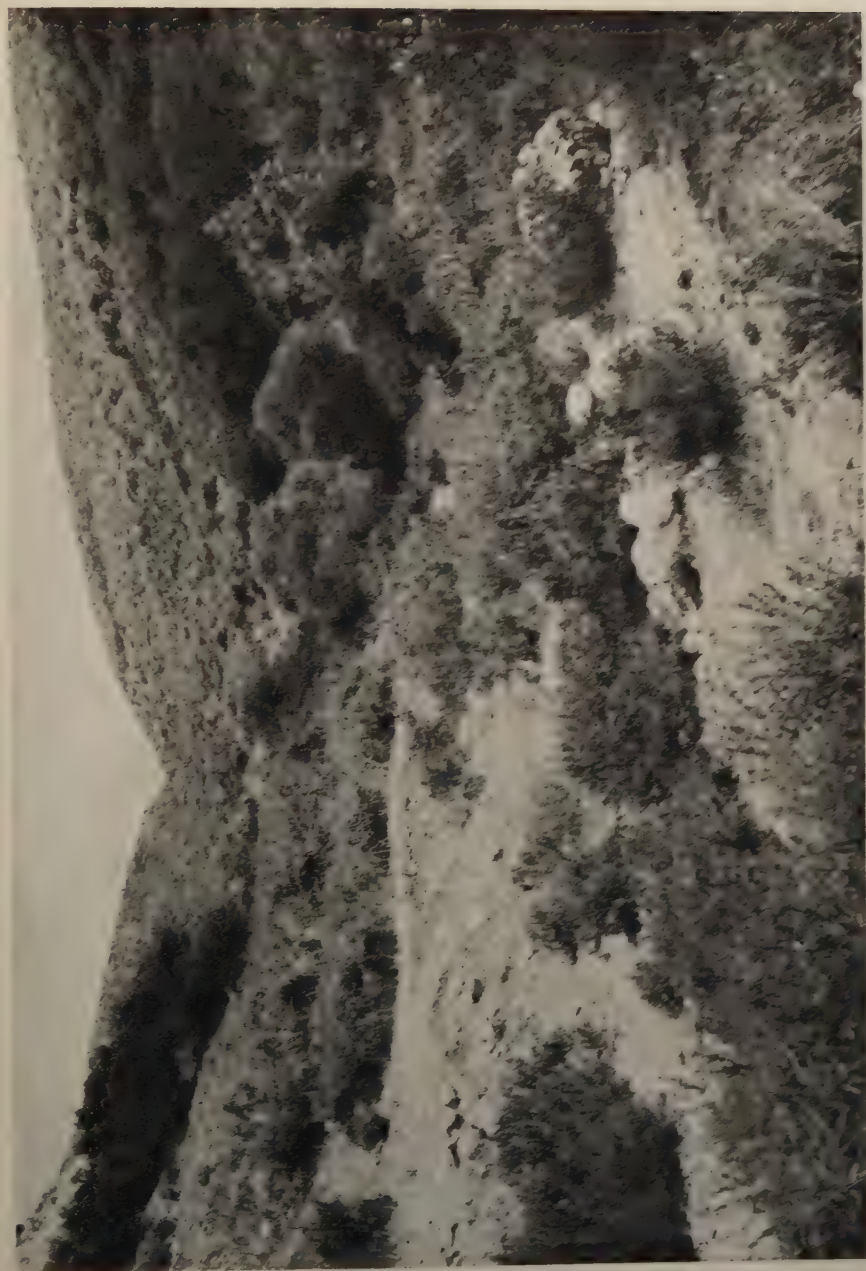The Galilean subassociation of the *Quercus calliprinos — Pistacia palaestina* association (Upper Galilee, near Meiron)

Figure 2

The typical subassociation of the *Quercus calliprinos—Pistacia palaestina* association (Samaria, Mt. Hetery; Photo Y. Wahrmann).

Figure 3

Partly destroyed maquis of the *Quercus calliprinos—Pistacia palaestina* association (Mt. Carmel, descent from Muhraka).

unknown in Israel and (2) the Hanita-Eilon variant which occupies lower altitudes and is consequently poorer in deciduous species.

Subassociation *typica* (Figures 2, 3) is the most common maquis type of Samaria and Mt. Carmel. It differs from subassociation *galilaea* by a series of characteristic species, such as *Ainsworthia carmeli*, *Viburnum tinus*, *Cytinus hypocystis*, *Euphorbia dendroides*, *Allium dumetorum*, *Saxifraga hederacea*, etc. In its floristic features it is intermediate between the *galilaea* and the *depauperata* subassociations.

Subassociation *depauperata* is the southernmost type of maquis in Israel. It is very poor in arboreal species and lianes. As it is adjacent to the sub-Mediterranean batha vegetation, it receives quite a number of species from the *Ballotetalia* order. The high frequency of *Hyparrhenia hirta* in this subassociation deserves special mention.

The phytosociological relationships of the components

Even under ideal conditions each plant community harbours, in addition to its characteristic species, a considerable number of species which are not exclusively characteristic of the community. The latter may be dicoenotic or polycoenotic. Very often are they neglected in literature and considered accidentals. In fact, a detailed analysis of the species of this category may be of help in tracing the history of the community. We have, therefore, laid stress on a more detailed phytosociological grouping of the species.

The association under review is exceptionally rich in species. This fact could at first glance be attributed to the favourable climatic and edaphic conditions of the habitat. However, an examination of the phytosociological composition shows that human interference is largely responsible for the present composition of the maquis. In stands that have escaped the destructive action of man, such as 'sacred woods' or 'closed forests', the number of species is considerably lower than in those which at one time or another have been disturbed by man.

The characteristics of the association, the alliance and the order, as listed in Table II, give an idea of the trees and shrubs which constitute the maquis as well as of its climbers and its herbaceous shade-demanding species. The latter comprise a series of rare ferns, annuals and plants some of which are not included in our list.

The presence in this community of so many associates of the order *Poterietalia* is due to the fact that many associations of this order are successional stages of the *Quercus–Pistacia* climax community. This applies in particular to many dwarf shrubs of the batha and garigue formations which linger within the oak community for as long as they manage to obtain sufficient light. The number of the components of the *Poterietalia* within the *Quercus calliprinos – Pistacia palaestina* association is also proportional to the extent of its destruction by man.

The considerable number of species of the *Varthemietea* class within the reviewed community is equally striking. This class comprises lithophytes and chasmophytes confined to rocky outcrops. The presence of such habitats in the midst of the maquis stands indicates that the maquis have been subject to extensive soil erosion and

denudation following deforestation. It also shows that soil regeneration considerably lags behind the recovery of the vegetation.

The number of ruderal and segetal species (*Rudereto-Secalinetea* class) is surprisingly large. This reflects the proximity of the maquis to cultivated soils, the conversion of maquis areas into cultivated lands and the 'ruderalization' of the maquis by man and his cattle for many centuries.

Of particular interest is the category of plants forming the initial stages in the successional seres of the *Quercetea* class. As a rule, these plants show a wide ecological amplitude which enables them to occur in many communities of the class. Whenever the natural conditions make it possible for the sere to progress normally, this group is rather ephemeral, but extensive destruction of the advanced stages of the sere favours the permanence of these plants in the interspaces of the shrubs.

ECOLOGICAL REMARKS

Stratification

The vertical stratification of the oak community is very incomplete. Where the trees and the high shrubs form a dense canopy, younger specimens of the same species, together with a few herbs, may form the underwood. While most of the trees and higher shrubs, as well as the climbing plants of the maquis tolerate considerable shading without injury, the bulk of the dwarf shrubs of the *Poterietalia*, which accompany the maquis, entirely succumb to overshadowing. Thus, dense stands of maquis are extremely poor in species. Generally, however, such pure maquis is very rare because throughout its entire area of distribution man is steadily interfering with the maquis and reduces its density, so that many photophilous plants of the batha and garigue, which find favourable growth conditions in the interspaces, form a lower stratum in the maquis.

Life Forms and Phenoecology

The number of phanerophytes in the maquis do not exceed 5% of the total number of species. Their number roughly equals that of the chamaephytes. The remaining 90% of species are distributed between the categories of therophytes, hemicryptophytes and cryptophytes, which together may be classified as winter plants or hyemophytes. The association under review comprises almost all the Mediterranean phanerophytes occurring in the country. Although the maquis is evergreen in its appearance, its evergreen phanerophytes are somewhat less numerous than the deciduous ones. Of the evergreens the following may be mentioned: *Quercus calliprinos, Phillyrea media, Rhamnus punctata, Rh. alaternus, Olea europaea* var. *oleaster, Pistacia lentiscus, Laurus nobilis, Arbutus andrachne, Ceratonia siliqua*. The deciduous trees and shrubs are: *Quercus infectoria, Qu. ithaburensis, Cercis siliquastrum, Crataegus azarolus, Acer syriacum, Pyrus syriaca, Prunus ursina, Amygdalus communis, Sorbus trilobata, Rhamnus palaestina, Styrax officinalis*. Evergreen spartoid components are: *Calycotome villosa, Spartium junceum, Gonocytisus pterocladus*.

Pheno-ecologically, the flora of the maquis should be divided into evergreen phanerophytes, deciduous phanerophytes, evergreen heterophyllous chamaephytes and hyemophytes. The fact that so many trees of the maquis are winter deciduous is very puzzling from the point of view of adaptation, because – judging from the behaviour of evergreen trees – local climate is most favourable for plant activity in winter. The interruption of physiological activity in the deciduous species during winter is to a certain extent discordant with the climatic rhythm of the area. This group is thus in a sense ecologically alien to the maquis, no doubt owing to their provenance from colder temperate regions. Most of them occur – or have their nearest relative – in continental non-Mediterranean regions. However, these deciduous trees are remarkable for their plasticity in the duration of their resting period which in warm winters may not last more than a month.

All the evergreen phanerophytes shed their leaves mainly in early summer. With the exception of *Ceratonia* they flower in spring and their fruit ripens in summer. *Ceratonia* flowers in summer and its fruit ripens after ten or more months. This, as well as the duration of cambial activity, the need for higher temperatures and relevant geographical data have elsewhere (Zohary 1951) led the author to suggest a tropical origin for *Ceratonia*.

The cambial activity of some local maquis trees has been studied by Fahn (1953). The following conclusions may be mentioned: In all the maquis trees investigated, whether deciduous or evergreen, cambial activity begins at the end of March. The only exception is *Ceratonia*, in which cambial activity starts in April. However, the period of bud-break is different in evergreen and deciduous trees. In deciduous trees buds sprout in February and March, in evergreens – in April. The duration of cambial activity varies with the species regardless of their being deciduous or evergreen. Duration of cambial activity was longest in *Ceratonia siliqua*, where it lasted from April till the following March. It was shortest – from March to July – in *Crataegus azarolus;* in other species it ceases between August and October. All the trees investigated by Fahn produce annual rings which comprise spring, summer and late wood in varying proportions. The smallest proportion of summer wood is produced by *Crataegus* and the largest by *Pistacia atlantica*. Available evidence does not show cambial activity to be determined by changes of temperature, nor can shortage of water supply be the cause of cessation of activity, since *Ceratonia siliqua* – which grows together with the other trees – shows cambial activity all the year round. The spartoid shrubs, with their evergreen stems and winter ephemeral leaves, are somewhat intermediate between the deciduous and the evergreen type. The spartoid type is not exclusively Mediterranean, it is also represented both in more mesic and in desert regions.

The chamaephytes present the most interesting life form in the maquis. They are generally evergreen, but their larger winter leaves are shed at the beginning of the dry period, when they are replaced by smaller, mostly scale-like summer-leaves. Thus, their activity is not interrupted but only considerably reduced in the dry

season. The rate of surface reduction may sometimes amount to 70–80% of the assimilating surface during winter (Orshan 1952). The remaining life forms are mainly winter plants and only a few hemicryptophytes continue their activity during summer. Among the cryptophytes, the geophytes are a very striking group in the maquis climax area with regard to their abundance and ecology.

Root Habits

The great majority of East Mediterranean maquis trees and shrubs possess an allorhizous root system, in which some of the long roots spread horizontally, close to the soil surface. The remaining roots may penetrate into the soil vertically, down to a depth of 2–5 metres or more. This has been observed in *Crataegus*, *Amygdalus* *Ceratonia*, *Quercus*, *Pistacia*, *Olea* and others. Such deep roots are frequent in fissures and crevices of rocks where fine soil has accumulated and where moisture is available throughout the year. These roots apparently supply the total moisture requirements of the plant during summer, as the horizontal roots are confined to soil layers mostly without available moisture in summer. The roots of many maquis plants are able to penetrate soft rocks. This is the case with *Ceratonia*, *Arbutus*, *Pistacia palaestina*, *P. lentiscus*, *Quercus calliprinos*, *Rhamnus palaestina* (Oppenheimer 1956). It should, however, be mentioned that germination of these plants is not possible on the bare rock, but requires a certain layer of soil or at least small cavities of the rocks filled with soil and moisture. Penetration into the rock occurs at a later stage of seedling development.

Regeneration

A significant feature of the maquis plants is their ability to regenerate vegetatively from subterranean dormant buds whenever they are cut or burned to the ground. It is due to this quick regeneration after destruction by fire and axe that so many large areas of maquis have been preserved to the present day, in spite of continuous destruction since time immemorial. At the same time, the high adaptivity of maquis trees and shrubs to their environment – living as well as inanimate – must be considered as due to continued selection. Thus the maquis, with its present floristic composition, is no doubt only a residue of a much larger species population unintentionally selected by man for their ability to recover from damage by fire, axe, browsing and denudation. Endowed with these qualities, the maquis was able not only to remain at equilibrium with man's continuous interference, but also to spread at the expense of the more mesic vegetation of adjacent altitudes.

Hydroecology

In view of the fact that the maquis of Israel is the southernmost outpost of the East Mediterranean woods which merges into steppe and desert, data on the water economy of local maquis trees and shrubs deserve particular attention.

Transpiration values

Transpiration studies on maquis trees by Oppenheimer (1953), Orshan (MS.) and Poljakoff (1945) have led to the following subdivision:

(a) Polyhydric plants, with a high transpiration intensity. This category chiefly comprises the deciduous constituents of the maquis. (b) Oligohydric plants, with a low rate of transpiration. This group includes most of the sclerophyllous evergreen trees and shrubs.

The following is a list of transpiration values, in milligrams of water lost per 1 gram fresh weight during 1 hour. The Roman figures in brackets indicate months of measurements.

Quercus calliprinos 678 (VIII, Mt. Carmel); *Ceratonia siliqua* 411, 510 (VIII, Mt. Carmel), 335 (III, Jerusalem), 244 (VIII, Jerusalem); *Amygdalus communis* 2200 (III, Jerusalem), 884 (IX, Jerusalem); *Olea europaea* 82 (III, Jerusalem), 231 (IX, Jerusalem); *Pistacia lentiscus* 300 (V, Mt. Carmel), 532, 323 (VIII, Mt. Carmel); *Rhamnus palaestina* 810 (V, Mt. Carmel), 840 (VIII, Mt. Carmel); *Crataegus azarolus* 870 (VIII, Mt. Carmel); *Calycotome villosa* 362 (VIII, Mt. Carmel).

Oppenheimer has studied the water relations of maquis trees in Samaria on Mt. Hetery, East of Zikhron Yaakov. He found a low rate of transpiration and a considerable decrease in summer rates in *Quercus calliprinos* and *Laurus nobilis* (oligohydric) and a higher one in *Pistacia palaestina* (meso- or polyhydric). In *Phillyrea media*, despite the dwindling water reserves of the soil, water loss was uniform throughout the year.

Osmotic values

Available data (Zohary and Orshan MS., Poljakoff 1945, Berlinger MS.) show the trees and shrubs of the maquis to be distinguishable into polybars and oligobars. The first group comprises plants in which the osmotic values for the summer exceed 30 atm, e.g. *Rhamnus alaternus* 39.2 (VII), *Phillyrea media* 40.1 (VII), *Olea europaea* 42.6 (XI). The second group comprises plants in which the summer values are below 30 atm, e.g. *Laurus nobilis* 27.2 (VII), *Arbutus andrachne* 26.6 (VII), *Pistacia palaestina* 21.8 (VIII), *Cercis siliquastrum* 19.9 (VII), *Quercus calliprinos* 20.3 (VIII), *Ceratonia siliqua* 20.2 (VIII), *Pistacia lentiscus* 19.6 (VIII), *Amygdalus communis* 24.7 (VIII), *Rhamnus palaestina* 23.1 (VIII), *Crataegus azarolus* 29.6 (VIII). All of these data were obtained in typical Mediterranean habitats, partly in the vicinity of Jerusalem and partly on Mt. Carmel. As far as these values reflect the hydrature of the plants, there is certainly no difference between evergreen and deciduous trees, except that all polybars are evergreens. The following data obtained by Oppenheimer (1953) roughly confirm the values quoted above: *Quercus calliprinos* 25.7 atm, *Laurus nobilis* 36.8 atm, *Pistacia palaestina* 24.7 atm, *Phillyrea media* 55.0 atm (all from Mt. Hetery, September and October). At the same locality, in what appeared

to be a moister habitat, Oppenheimer (l.c.) obtained the following figures: *Ceratonia siliqua* 14.1 atm, *Quercus calliprinos* 20.9 atm, *Pistacia palaestina* 24.6 atm, *P. lentiscus* 24.4 atm, *Styrax officinalis* 37.5 atm, *Phillyrea media* 49.2 atm.

Resistance to saturation deficits

This has been studied by Berlinger (MS.), who obtained the following results: (a) The leaves of maquis trees and shrubs do not show uniform values of water deficits. Low deficits were found in *Ceratonia siliqua, Pistacia palaestina, Quercus calliprinos, Pistacia lentiscus, Styrax officinalis*, the lowest (20–23%) occurring in latter three. *Amygdalus communis* and *Crataegus azarolus* showed medium deficits and *Olea europaea, Phillyrea media* and *Rhamnus palaestina* very high ones (53.8%, 66.7% and 69.7% respectively). The first group comprises both deciduous species and evergreens. Their mean daily deficit during the dry period does not exceed 15%. The second group shows a summer average of about 21% and a mean daily maximum of 30–34%. The high-deficit group comprises evergreens only, showing during the dry season an average deficit of 31.7% and a mean daily maximum of 44%. (b) Some of the maquis trees and shrubs (e.g. *Phillyrea, Olea* and partly also *Crataegus*) have very low deficits (0–15%) on winter mornings and rather high deficits (25–50%) on summer mornings. The remaining species have low deficits (5–20%) in the mornings of both summer and winter. (c) Almost all plants have winter deficits considerably below those of the summer ones.

The above data permit the following conclusions to be drawn: In general the maquis plants are true xerophytes, with a decrease in the transpiration rate and an increase in the water deficit of their leaves in the course of summer. While the differences in transpiration behaviour of various species undoubtedly have a genetical basis, there may be considerable differences between individuals of the same species in the same habitat which must be ascribed to the uneven distribution of moisture in the substrate, as well as to the size and depth of the soil pouches from which the roots derive moisture and nutrients.

By comparison with the vegetation of steppe and desert, the Mediterranean maquis should be considered as highly drought resistant, because (1) maquis trees and shrubs do not reduce their transpiring surface in the dry period; (2) they remain active in summer; (3) they do not lose their water in the manner characteristic of desert and steppe plants which attain deficits of 60–70% and consequently become almost inactive during the dry period.

Thermoecology

Resistance of local trees and shrubs to high temperatures was studied by Konis (1949), who found that the maximum temperatures which leaves tolerate under natural conditions are considerably lower than the lethal temperatures under experimental conditions. It has further been shown that lethal temperatures are lower for younger than for fully developed leaves, and that deciduous plants are less heat

resistant than evergreens. These data warrant the conclusion that as far as the maquis is concerned, heat in itself is not a damaging factor, even though under natural conditions maquis plants are exposed to summer temperatures as high as 40° or 45°C.

FLORISTICS AND PHYTOGEOGRAPHY

The association of the evergreen oak maquis is perhaps the richest plant community of the country. The original field list of this association contains no less than 200 species, some of which are endemics. A phytogeographical analysis of the components with high and medium presence reveals the following relations:

Omni-Mediterranean	40 species (31%)
East Mediterranean	48 species (38%)
North Mediterranean	4 species (3%)
Mediterranean–Irano-Turanian	21 species (17%)
East Mediterranean–Irano-Turanian	8 species (6%)
Eurosibero–Boreoamerican– Mediterranean–Irano-Turanian	4 species (3%)
Borealo–Tropical	1 species (1%)
Mediterranean–Irano-Turanian– Saharo-Sindian–Tropical	1 species (1%)

As already pointed out above, most species of this association reach their southern limit of distribution rather abruptly, even though individual species reach their limits at different latitudes. Moreover, many of those species do not recur in Mediterranean North Africa, e.g. *Styrax officinalis, Crataegus azarolus, Amygdalus communis, Cercis siliquastrum, Arbutus andrachne, Pistacia palaestina, Quercus calliprinos, Qu. infectoria, Prunus ursina, Rubus tomentosus, Acer syriacum, Rhamnus palaestina, Rh. punctata, Salvia triloba*. This is undoubtedly due to the desertic wedge which protrudes northwards, almost to the shore of the Mediterranean in the Sinaitic-Lybian area (Sinaitic-Lybian gap). It is believed that this desert "peninsula" in the Mediterranean region has already existed in the Late Pliocene. Ever since, it has been a serious obstacle to mutual floral exchange between S. Western Asia and North Africa, especially at the time when the Mediterranean maquis has established itself in the East Mediterranean following the regression of the Tethys. The striking difference in the composition of the maquis of North Africa and Israel warrants the assumption that the maquis of North Africa has obtained its Mediterranean element directly from the NW Mediterranean, whereas the maquis of Israel has obtained this element from the NE Mediterranean.

It is significant that more than 70% of the arboreal components of the maquis of Israel belong to the East Mediterranean element or to the East Mediterranean–Irano-Turanian group in the wide sense. It is this group of plants from which the East Mediterranean maquis derives its individuality, and which separates it from its West Mediterranean counterpart. Of the East Mediterranean phanerophytes which are leading plants and main associates, the following may be mentioned: *Quercus*

calliprinos, Pistacia palaestina, Rhamnus palaestina, Rh. punctata, Acer syriacum, Styrax officinalis, Prunus ursina, Quercus ithaburensis.

Mention should also be made of the Irano-Turanian influence reflected in a not inconsiderable number of Mediterrano–Irano-Turanian biregionals—in excess of 20%—which occur in the maquis. These include among others: *Quercus infectoria, Pyrus syriaca, Amygdalus communis.* The relationship between the East Mediterranean maquis and the Irano-Turanian region is further indicated by maquis plants which penetrate into the Irano-Turanian region, e.g. *Crataegus azarolus, Rubia olivieri, Juniperus oxycedrus, Jasminum fruticans* and others.

The group of the omni-Mediterranean and sub-Mediterranean species is nevertheless considerable. It consists mainly of evergreen plants and climbers, such as *Laurus nobilis, Ceratonia siliqua, Phillyrea media, Pistacia lentiscus, Rhamnus alaternus, Prasium majus, Spartium junceum, Lonicera etrusca, Clematis flammula, Ruscus aculeatus, Asparagus aphyllus, Tamus communis, Smilax aspera, Cistus villosus, C. salvifolius.* The leading plants of this association, *Quercus calliprinos* and *Pistacia palaestina*, have their West Mediterranean vicariads, in *Quercus coccifera* and *Pistacia terebinthus.* Similarly, *Arbutus andrachne* is an East Mediterranean vicariad of the mainly West Mediterranean *A. unedo.*

<div align="center">SYNGENESIS</div>

The Problem of the Climax

The question whether the maquis—so common in and characteristic of the Mediterranean countries—concludes the successional sere or is but a pre-final stage of this sere, has been extensively discussed, notably in connection with the Western Mediterranean. In the area under review the following facts are relevant to this question:

(1) When not interfered with by man, all shrubs of the maquis may grow into well-developed trees. *Quercus calliprinos* frequently grows into a tree 10–15 m high, with a thick trunk. Outstanding specimens of this species occur in the so-called "sacred woods" of Israel and of other East Mediterranean countries. Isolated lofty oak trees, associated with holy sites of the Moslems and sometimes traceable to earlier cultures, may be found even under rather unfavourable climatic and edaphic conditions (Wadi Waran, Transjordan, Figure 4). *Crataegus azarolus, Laurus nobilis, Pistacia palaestina* may also grow into rather high trees. This is perhaps the best proof that the commonly prevailing bushy form of the maquis is but a penultimate succession stage permanently maintained by man and his cattle.

(2) Whenever maquis stands are unaffected by man and allowed to grow by themselves their composition changes from a rich mixture of species to an almost pure stand of *Quercus calliprinos.* This is the case in the *Quercetum* of Jebel Druze (Syria), as well as in several localities in the Lebanon Mountains, on Mt. Carmel (the Wood of the Forty), on Mt. Meiron (Sartaba), and in the Judaean Mountains in the

environs of Hebron ("Mamre oaks" of the Bible) and Jerusalem (Aqua-Bella). This justifies the assumption of an additional association—*Quercetum calliprini*—to be included within the alliance of *Quercion*. As this forest association is very fragmentary, we are unable to say anything of its composition and ecology.

Figure 4

A "sacred oak" (*Quercus calliprinos*) amid a desolate landscape (Eastern Gilead, Wadi Waran).

Succession

For the past twelve years the author and his colleagues have observed the plant succession in abandoned fields on terraces of the Judaean Mountains. These mountains, characterized by the *Quercus calliprinos* maquis, have been under terrace cultivation for centuries. The edges of each terrace show remnants of the primary vegetation consisting, among others, of *Quercus calliprinos*, *Crataegus azarolus*, *Rhamnus palaestina*, *Pistacia palaestina*, all of which bear fruit. The shrubs are accompanied by batha and garigue components, such as *Poterium spinosum*, *Thymbra spicata*, *Thymus capitatus*, *Cistus villosus*, *C. salvifolius*, *Calycotome villosa*, *Salvia triloba*. Some of these terrace fields have been abandoned in 1947 and exposed to undisturbed revegetation by plants growing on the edges of the terraces.

Even though seeds of all maquis plants growing on the margins were available in profusion, revegetation of the terraces did not start with arboreal species but followed a certain orderly succession. The weed flora which has accompanied the crops for generations did not entirely disappear following the cessation of cultivation. Many annual and perennial weeds persisted in the fields for two or three years after fallowing. During the following 2–3 years this flora was, at least on terra rossa, gradually but not exclusively replaced by a therophytic and hemicryptophytic pioneer

flora, which constitutes the first successional stage of an agrosere. Many annuals of this stage appear in the above analytical table under the heading "Pioneers of the *Quercetea*". Among the hemicryptophytic species mention should be made of *Carlina involucrata, Echinops viscosa, Psoralea bituminosa, Oryzopsis holciformis, Dactylis glomerata, Hordeum bulbosum, Phalaris tuberosa.* In rendzina soils this "pioneer stage" may be partly or entirely missing. The first dwarf shrub association which establishes itself on terraces in succession to the herbaceous stage is the *Poterietum spinosi*, followed—as a rule—by *Cistetum*. According to Orshan (verbal information) the *Cistus salvifolius* and sometimes *C. villosus* shrubs require some shade in their early stages, and this shade is provided by *Poterium*. The *Cistus* shrubs with their rather rapid growth may sooner or later overtop the shrubs of *Poterium*, which succumb to overshading and leave *Cistus* as the dominant species.

The herbaceous pioneer stage, the *Poterium* stage and that of *Cistus*, are the most common stages in the early development of the sere. However, for reasons which are not yet clear, deviations from the above sequence may occur locally. Thus, *Poterium* may persist for a long time without being replaced by *Cistus*, or else *Cistus* may occupy the field without being preceded by *Poterium*. In any case, in 12 years of observation, *Quercus calliprinos*—the most common species on the edges of the terraces—has nowhere been able to penetrate the areas of revegetation. Though viable seeds of oak were abundant, we failed to find even a single seedling of oak or any other trees amid the established *Poterietum* and the *Cistetum* of the terraces. Acorns artificially sown beneath shrubs of *Poterium* or on barren ground failed to germinate even though numerous seedlings were found under the branches of oaks and pistacias, where the soil is rich in humus and sufficiently moist to maintain the seedlings throughout the year.

Evidently, the reestablishment of the arboreal elements of the climax community requires much time even if denudation, which generally follows deforestation, is prevented by terracing. In the area concerned, it is for the time being impossible even to estimate the span of time required for the climax components to reestablish themselves. Soil conditions evidently require much improvement in both humus and moisture content, to warrant germination and establishment of seedlings under the cover of the dwarf shrubs.

On the other hand, the occurrence in Israel and elsewhere of maquis trees in definite age groups may lead to the assumption that germination and establishment of the arboreal components of the maquis within the sere require particular climatic conditions which may occur only in very rainy years or after two or more consecutive years of heavy rains or of otherwise unusual climatic conditions.

Climax Changes

In areas where deforestation has been followed by extensive soil erosion and denudation, the arboreal climax vegetation, once destroyed, may under prevailing climatic conditions never be able to reestablish itself. In the Mediterrano–Irano-Turanian

borderland, where torrential rains following deforestation may destroy the soil profile, destroyed climaxes are practically irreversible. Thus the beautiful trees of *Quercus calliprinos* in Wadi Waran (Transjordan), *Pistacia atlantica* in the Negev, *Juniperus phoenicea* in Sinai, *Cupressus sempervirens* in Edom, all indicate the climax vegetation of their respective areas. But they are isolated "as the juniper in the wilderness" and in their present extremely desolate environment they do not possess any power for regeneration. Such trees and stands should be looked upon as remnants or relics of climax communities of a former period, which was more favourable for the growth of trees either climatically or edaphically. Consequently, even without assuming climatic changes within historical times, the reestablishment of a destroyed climax community may be prevented solely by the destruction of soil following deforestation. This is because soil may require geological periods for its restoration. Therefore, in marginal areas, past and present climax vegetation should be distinguished. Whereas the former may be deduced from existing remnants, these do not quite warrant predictions of the actual climax vegetation in the area concerned. However, given time and suitable (eu-Mediterranean) conditions, the possibility of reestablishment of arboreal vegetation should not be excluded. In Israel there occur cemeteries, remnants of olive tree groves, wine and oil presses in the midst of dense maquis and forest (e.g. Tiv'on, Nahal Qarn, Mt. Meiron), which prove that the present vegetation has reestablished itself time and again on abandoned agricultural land.

MAN AND MAQUIS

As elsewhere in the Mediterranean region, man has very early interfered with the natural vegetation in a variety of ways, by cutting trees for housing, fuel, charcoal production, lime kilns and household industry, etc. Yet the demand for timber may well have been less damaging to the vegetation than the browsing by goats, and it is certainly browsing which by its particular mode of injuring trees converts the trees into maquis shrubs. In the area under discussion, destruction of forests was largely accelerated by the timber requirements of the nomads living in the adjacent treeless desert, who from time to time have invaded large stretches of land and carelessly destroyed its arboreal vegetation.

Yet in Israel, as elsewhere, preparation of land for agriculture was the main cause of forest destruction. Deforestation started long before the dawn of history. It has been going on for millennia, and is still practiced. In fact, it is surprising that in spite of a long history of destruction rather large stretches of maquis have been preserved to this day. Many arboreal species would certainly not have survived if they had been unable to regenerate vigorously from subterranean shoots to which man's tools had no access, and if they were unable to produce long and deep roots to supply moisture during the dry summer from rock crevices. The primitive tools which were used until recently spared obviously many trees which are easily de-

stroyed by modern equipment. Not infrequently, man's fight against the forest was unsuccessful, as may be judged from the many remnants of maquis which man has unwillingly left in the midst of the fields. Many agricultural areas in Upper Galilee have a sprinkling of stunted oaks, pistacias, hawthorns, buckthorns, storaxes, etc. The introduction of modern tools is a serious menace to the local maquis vegetation and in particular to the *Quercus calliprinos – Pistacia palaestina* association.

REEERENCES

ASHBEL, D., 1951, *Regional Climatology of Israel*, Meteorol. Dept., The Hebrew University of Jerusalem.

BERLINGER, Z., 1956, Water deficit in the Mediterranean maquis of Mt. Carmel (unpublished).

EIG, A., 1938, On the phytogeographical subdivision of Palestine, *Palest. J. Bot. Jerusalem*, **1**, 4–12.

EIG, A., 1946, Synopsis of the phytosociological units of Palestine, *Palest. J. Bot. Jerusalem*, **3**, 183–246.

FAHN, A., 1953, Annual wood ring development in maquis trees of Israel, *Palest. J. Bot. Jerusalem*, **6**, 1–26.

KONIS, E., 1949, The resistance of maquis plants to supramaximal temperatures, *Ecology*, **30**, 425–429.

OPPENHEIMER, H. R., 1953, An experimental study on ecological relationships and water expenses of Mediterranean forest vegetation, *Palest. J. Bot. Rehovot*, **8**, 103–124.

OPPENHEIMER, H. R., 1956, Pénétration active des racines de buissons méditerranéens dans les roches calcaires, *Bull. Res. Counc. of Israel*, **5D**, 219–222, 2 pls.

ORSHAN, G., 1954, Surface reduction and its significance as a hydroecological factor, *J. Ecology*, **42**, 442–444.

POLJAKOFF, ALEXANDRA, 1945, Ecological investigations in Palestine. I. The water balance of some Mediterranean trees, *Palest. J. Bot. Jerusalem*, **3**, 138–150.

ZOHARY, M., 1951, The arboreal flora of Palestine and Transjordan and its ecological and phytogeographical significance, *Imp. For. Inst. Oxford, Inst. Pap.*, **26**, 1–59, 1 map.

ZOHARY, M., 1955, *Geobotany*, Sifriath Poalim, Merhavia (in Hebrew).

ZOHARY, M., 1960, *Plant Life of Palestine (Israel and Jordan)*, Ronald Press, New York (in press).

ZOHARY, M. AND ORSHAN, G., 1959, The maquis of *Ceratonia siliqua* in Israel, *Vegetatio*, **8**, 285–297.

DIATOMEAE AND CYANOPHYCEAE OCCURRING ON DEEP-WATER ALGAE IN THE HAIFA BAY AREA

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ABSTRACT

The benthonic Diatomeae and Cyanophyceae found as epiphytes on deep-water algae or occurring on experimental panels for antifouling paints in the Haifa Bay area are described. These include 42 species of Diatomeae and 11 species of Cyanophyceae. The distribution of species is considered in relation to the various depths and types of sea bottom occurring in this region. The environmental origin of some of the species recorded in the material which are not characteristically benthonic is dealt with.

INTRODUCTION

The large scale collections of benthonic material carried out in the Haifa Bay area during the years 1953–56 by dredge and bottom grab included many forms of macroscopic algae, which are now being processed and identified (Edelstein, in preparation).

The numerous genera and species of algae form definite associations in the various types of sea bottom constitution in this area, whose composition includes loams, sands, rocks and gravel. It was felt that a survey of the microscopic algae would be useful, in order to contribute towards a better knowledge of this region. Moreover, while planktonic diatoms, dinoflagellates and other pelagic groups have been fairly thoroughly investigated over a number of years in the course of fisheries and marine hydrobiological studies (Komarovsky, in preparation), the survey of benthonic microscopic algae, especially those occurring at greater depths has, so far, not been undertaken.

It is not only along the Israel shores that insufficient attention has been paid to this very varied biotope. If one glances at the pertinent literature, one is impressed by the scantiness of works dealing with the distribution of algae in general, and microscopic benthonic ones in particular, at depths greater than the immediate littoral belt along the various sea coasts.

The reason for the limited investigations in this field becomes apparent when one

considers the difficulties involved in field work which necessitates the use of a boat, an experienced crew and adequate sampling equipment. The present work was made possible as a result of the combined physical, chemical and biological survey of the Haifa Bay area undertaken by the staff of the Sea Fisheries Research Station, Haifa, during the years 1953–56. The material examined by the authors in the course of this study has been kindly put at their disposal by Dr. E. Gottlieb from the same institute, who personally supervised the collection of samples from the sea bottom. Also included in this study are the results of observations carried out on experimental panels in Haifa and Kishon Harbours in connection with a marine antifouling paints research project (Komarovsky and Schwarz 1957, 1959).

MATERIAL AND METHODS

The dredge and bottom grab samples from which the algae were collected at 14 different stations were distributed over the Haifa Bay area at different depths and with varying types of sea bottom. In the following table the types of sea bottom and depths in fathoms at each station are indicated:

TABLE I

Stations in Haifa Bay area—depths and types of sea bottom

No. of station	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Depth in fathoms*	13	16	17	20	29	40	21	19	24	45	48	30	15	10
Type of sea bottom	f.s	r;f.s.	f.s	g;s.m	r;m	m	s.m	r;s.m	s.m	m	m	m;g	sh;c.s	r

    * 1 fathom = 1. 8m; f.s = *fine sand*; c.s. = *coarse sand*; sh = *shells*; r = *rocks*; m = *mud*; g = *gravel*; s.m = *sandy mud*.

The dredge was pulled from one station to the next for a period of 10–15 minutes.
    The dredge and bottom grab samples after being hauled on board the vessel were thoroughly washed with a powerful stream of water from a rubber hose in order to separate the p'ant and animal groups from the accompanying bottom material. It is thus inevitable that a large proportion of microscopic organisms, including benthonic diatoms and other groups, was lost in this process. Nevertheless, subsequent analysis of the water obtained by washing and rinsing of the sea weeds in the laboratory revealed the presence of numerous species and individuals of these types which had been attached to the substrate. The material used for microscopic work was obtained by sieving the rinsing water through the bucket of a small plankton net (diameter of mouth 25 cm) whose bottom was covered with a piece of No. 25 bolting silk.

SYSTEMATIC LIST OF DIATOMEAE AND CYANOPHYCEAE ENCOUNTERED IN THIS INVESTIGATION

DIATOMEAE CENTRICAE

Coscinodiscaceae
1. *Coscinodiscus divisus* Grunow
2. *Coscinodiscus radiatus* Ehrb.
3. *Hyalodiscus stelliger* Bailey
4. *Melosira dubia* Kütz.

Actinodisceae
5. *Actinoptychus splendens* (Schadb.) Ralfs

Solenieae
6. *Guignardia flaccida* (Castr.) Perag.
7. *Rhizosolenia fragilissima* Berg.

Biddulphieae
8. *Bellerochea malleus* (Bright.) van Heurck var. *biangulata* Perag.
9. *Biddulphia pulchella* Gray
10. *Triceratium favus* Ehrb.

DIATOMEAE PENNATAE

Tabellariae
11. *Climacosphenia moniligera* Ehrb.
12. *Licmophora ehrenbergii* (Kütz.) Grunow var. *angustata* Grunow
13. *Licmophora flabellata* (Carm.) Agardh
14. *Licmophora juergensii* Agardh var. *constricta* Grunow ad interim
15. *Licmophora reichardtii* Grunow
16. *Grammatophora marina* (Lyngb.) Kütz.
17. *Grammatophora oceanica* Ehrb.
18. *Grammatophora undulata* Ehrb.
19. *Rhabdonema adriaticum* Kütz.
20. *Striatella interrupta* Ehrb.

Fragilariae
21. *Bacillaria paradoxa* Gmel.
22. *Fragilaria hyalina* (Kütz.) Grunow
23. *Podocystis adriatica* Kütz.
24. *Synedra gaillonii* (Bory) Ehrb. var. *major* n. var.
25. *Synedra hennedyana* Greg.
26. *Synedra undulata* Bailey
27. *Thalassiothrix frauenfeldii* Grunow

28. *Thalassiothrix longissima* Cleve et Grunow
29. *Thalassiothrix nitzschioides* Grunow

Cocconeidae

30. *Anorthoneis excentrica* Donk.) Grunow
31. *Campyloneis grevillei* (W. Sm.) Grunow
32. *Cocconeis britannica* Naegeli

Achnantheae

33. *Achnanthes brevipes* Agardh
34. *Achnanthes longipes* Agardh

Naviculae

35. *Nitzschia sigma* Kütz.
36. *Diploneis bombus* Ehrb.
37. *Diploneis crabro* Ehrb.
38. *Diploneis fusca* (Greg.) Cleve var. *aestiva* (Donk.) Hustedt
39. *Diploneis incurvata* (Greg.) Cleve
40. *Diploneis smithi* (Bréb.) Cleve
41. *Amphora commutata* Grun.

Campylodiscoideae

42. *Campylodiscus decorus* Bréb.

<div align="center">CYANOPHYCEAE</div>

Chroococcales

43. *Chroococcus turgidus* (Kütz.) Naeg.
44. *Synechocystis aquatilis* Sauv.
45. *Xenococcus schousboei* Thur.

Hormogonales

46. *Calothrix confervicola* (Roth) Agardh
47. *Lyngbya aestuarii* (Mert.) Liebmann
48. *Lyngbya agardhii* Gom.
49. *Lyngbya confervoides* C. Agardh
50. *Oscillatoria limosa* Ag.
51. *Oscillatoria margaritifera* Kütz.
52. *Oscillatoria nigro-viridis* Thwaites
53. *Spirulina subsalsa* Oerst.

<div align="center">DESCRIPTIONS OF SPECIES WITH NOTES ON THEIR DISTRIBUTION</div>

<div align="center">DIATOMEAE CENTRICAE</div>

1. *Coscinodiscus divisus* Grunow

Valves slightly convex with rows of areoles converging form the margin towards
the centre in poorly defined sectors. In individual sectors the rows of areoles parallel

to each other. The areoles bordering the margin are slightly smaller than those in the central and in the main area. Diameter of cell 96μ.

Rare, found only once on April 24th, at Station 14 close to the harbour area.

Distribution: The species has been recorded, according to Hustedt (1927–1933), from only a few widely distributed localities (Finnish coast and Villefranche-sur-Mer n the Mediterranean).

2. *Coscinodiscus radiatus* Ehrb.   (Plate I Figure 1)

Valves coin-shaped, generally flat. Rows of areoles radiating from centre towards the margin of the cell without any grouping in sectors. Diameter of cell 187μ.

This species has been frequently found in the plankton samples of the Israel coast. In our material it was found only once, in November 1955, at Station 14.

Distribution : Cosmopolitan, recorded from northern, temperate, subtropical and tropical marine environments.

3. *Hyalodiscus stelliger* Bailey

Cells short, cylindrical, 70μ in diameter; valves rounded.

Found on two occasions in dredge samples between Stations 5 and 6 in May 1956 and between Stations 14 and Harbour in April 1956. At both localities there was a predominance of *Halimeda tuna* among the macroscopic algae. Its occurrence both in relatively shallow water and at greater depths suggests a certain preference of this species to this particular type of substrate. On the other hand, *H. stelliger* was frequently found in the plankton samples collected over a number of years along the Mediterranean coast of Israel (Komarovsky, in preparation). It occurred always as single cells both in bottom and plankton samples.

Distribution : Generally regarded as a cold water species; found in the North Sea, northern Atlantic, western European coast, but previously rarely reported from the Mediterranean. Its frequent occurrence in the plankton of this region, however, does not seem to confirm this view. Reported also from the Suez Canal (Ghazzawi 1939).

4. *Melosira dubia* Kütz.

Cells circular, usually in process of division. No projection of any kind on the valve side. Diameter of cells 37μ.

Common, frequently found as epiphyte on *Dasya rigidula* in July 1958, at Station 14. Also frequently found on raft tests on experimental panels in the Kishon Harbour adjoining the Bay of Haifa (Komarovsky and Schwarz 1959).

Distribution: Recorded from the European coastal waters.

### 5. *Actinoptychus splendens* (Schadb.) Ralfs

This beautiful diatom is easily recognized by its radially undulating valves divided into raised and depressed sectors. The raised sectors have a stout apicule on the margin, contiguous with a narrow hyaline area extending towards the centre. No such structures present on the depressed sectors, which end distally in a narrow hyaline region parallel to the margin of the cell. Central area smooth with projections running into the lower part of the depressed sectors. Margin of cell regularly striated. Diameter of cell 70μ.
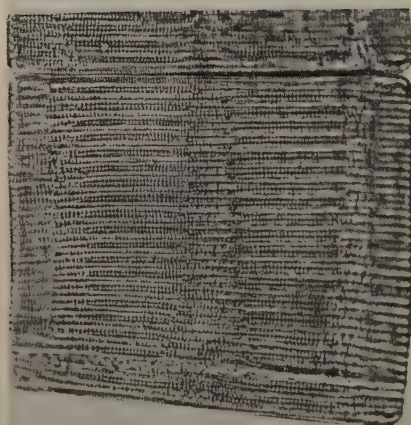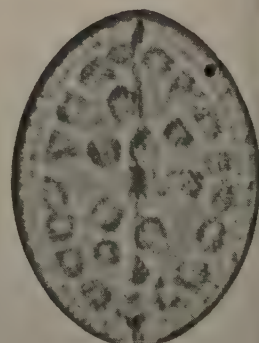
1
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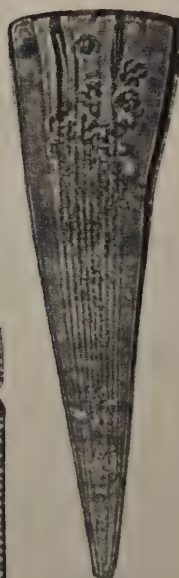
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Plate I

1. *Coscinodiscus radiatus.* 2. *Striatella interrupta.* 3. *Licmophora juergensii* var. *constricta;* 3a girdle view, 3b valve view. 4. *Rhabdonema adriaticum.* 5. *Cocconeis britannica.*

Found only once, in May 1956, between Stations 2 and 14.

Distribution: Cosmopolitan, common, frequently found in the Mediterranean.

6. *Guignardia flaccida* (Castr.) Peragallo

Cells cylindrical, solitary, with numerous transverse, wavy, intercalary bands. Cell wall weakly siliceous. Diameter of cell 100μ, length 280μ.

Found in August 1955 between Stations 8 and 9.

Distribution: Recorded from the littoral plankton of the Mediterranean and Atlantic coasts of Europe; also from the Gulf of Eilat (Aqaba) in October 1958 (Komarovsky, in preparation).

7. *Rhizosolenia fragilissima* Berg.

Cells elongated with a diameter of 87μ; transparent with very thin and weakly silicified cell-wall $(3–4\mu)$. Transverse, ring-shaped bands at both ends of the cell, which are fragile and hard to detect

Several specimens were found as single cells between Stations 8 and 9, in August 1955.

Distribution: A northern and temperate species rarely found in the western Mediterranean (Pavillard 1925).

8. *Bellerochea malleus* (Bright.) van Heurck var. *biangulata* Peragallo

Cells 90μ long and 22μ wide, united by valve surface to form ribbon-like chains. Valves weakly silicified. Apertures present only near margin of cells; central area closed by protuberances on valve sides. The form occurring in our material corresponds with var. *biangulata* Peragallo judging by size and shape of cells (Ioannou 1949).

Found only once, in May 1955, between Stations 8 and 9.

Distribution: A neritic species found in the coastal areas of the southern North Sea, Atlantic European coast and recently from the Mediterranean in the vicinity of Naples Bay and Rhodes Islands (Ioannou 1949). Lebour (1930) mentions its presence also in the Indian Ocean

9. *Biddulphia pulchella* Gray   (Plate II Figures 8 and 9)

Cells cylindrical, solitary or in chains, very variable in length from almost as long as, to several times longer than broad. Corner processes rounded and slightly higher than the bulge on the central region of the valves. Short spines present on bulge. Valves crossed by 5–6 transapical ribs. Small pores arranged in rows cover the whole surface of the cell. Similar pores cover even the contact regions of two adjoining young cells in the process of division. Apical length $180–212\mu$; length of girdle band $57.5–86\mu$; breadth $112–150\mu$.

Very common. Found in large numbers in February 1956 between Stations 2 and 7.

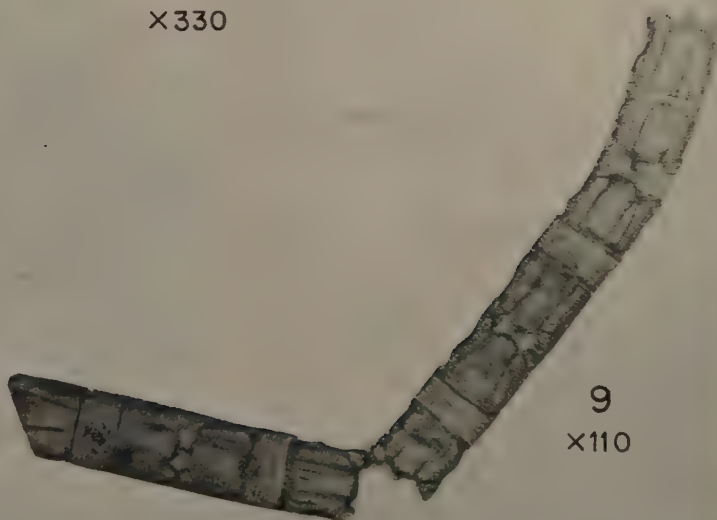*Distribution:* Reported from the Atlantic coasts of Europe and Pacific coast of America.
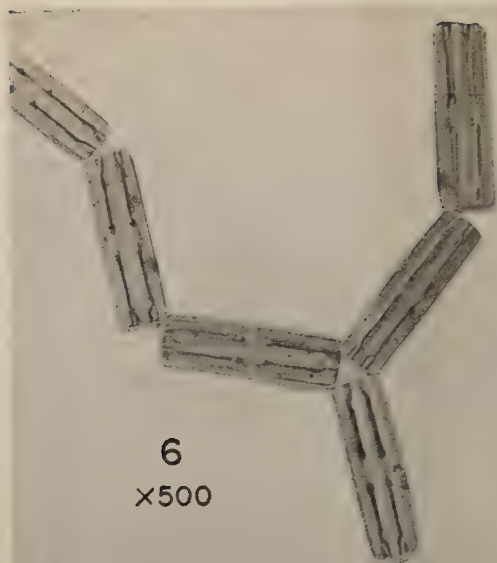
Plate II

6. *Grammatophora oceanica*. 7. *G. undulata*. 8. *Biddulphia pulchella*. 9. *B. pulchella*, chain formation.
10. *Diploneis crabro*.

10. *Triceratium favus* Ehrb.   Syn.: *Biddulphia favus* Ehrb.

Cells short, almost as long as broad, generally three-cornered with thick walls. Valve surface covered with hexagonal areoles arranged in rows.

Found in our material only once between Stations 11 and 12 in November 1955.

Distribution: A neritic species, widespread, recorded from the North Sea, European coast, Mediterranean, Suez Canal.

PENNATAE

11. *Climacosphenia moniligera* Ehrb.

Cells club-shaped with valves distinctly rounded at both ends. In valve view rectangular to rounded chambers in the upper region which gradually become elliptical to irregular towards the lower elongated foot. Length 340μ; breadth at upper region 25μ, at lower region 15μ.

Rare. Found only once in April 1956 at Station 14.

Distribution: A warm-water species, also reported from the Mediterranean.

12. *Licmophora ehrenbergii* (Kütz.) Grunow var. *angustata* Grunow

Cells wedge-shaped in girdle view with upper rounded end and blunt lower one. Intercalary bands converging towards the centre in the upper region of the cell, almost parallel in central region, slightly approaching one another in the lower region of the cell. Length 69μ, breadth at upper end 30μ.

Very common, found in large numbers in most of the samples between Stations 2 and 14.

Distribution: A neritic species, frequently reported from the European coasts including the Mediterranean. Reported by Aleem (1950 b) from Port Said and El-Arish.

13. *Licmophora flabellata* (Carm.) Agardh

Valves club-shaped with bulbose rounded lower end, gradually widening towards the upper end; pseudoraphe; valves cross-striated. Length 175μ, breadth in upper part 10μ.

Found in colonies on *Halimeda tuna* at Station 14.

Distribution: Known as a littoral species from the European coasts including the Mediterranean.

14. *Licmophora juergensii* Agardh var. *constricta* Grunow ad interim

(Plate I Figures 3a and 3b)

Cells wedge-shaped in girdle view, flaring abruptly in the upper third on one side and almost straight on the other; intercalary bands extend almost to lower end of frustules. Upper corners almost angular (approx. 70°–75°), ower end straight. In valve view club-shaped, upper end rounded while lower end slightly swollen. Between upper third and quarter of the length a pronounced constriction is present which is characteristic of this organism. All along the valves, fine striae perpen-

dicular to the pseudoraphe. Length 185–245μ, maximum breadth in girdle view 65μ; at lower end 7μ; in valve view above constriction 17.5μ, at constriction level 10.5μ; below constriction 13μ.

Rare. Found only in May 1955 between Stations 2 and 14 and in August 1955 near Station 9.

Distribution: A littoral species reported from the European coasts.

15. *Licmophora reichardtii* Grunow

Cells wedge-shaped in girdle view, with rounded ends; a slight gradual constriction present in valve view in the middle region of the upper half. Lower half of the valve gradually attenuates towards the lower end. Narrow pseudoraphe present. Length 224μ, breadth in valve above constriction 18μ, at constriction level 12μ, below constriction 13μ. In girdle view at upper end 32μ, at lower end 6.5μ.

Rare. Found only once in August 1955 near Station 9.

Distribution: Recorded from the Mediterranean, Adriatic and Black seas.

16. *Grammatophora marina* (Lyngb.) Kütz.

Cells slightly bent in girdle view and elliptical with slightly swollen ends in valve view. Septa with pronounced single curvatures near the margin of the cell. Length 85μ, breadth 20μ.

Rare. Found only once in May 1956 near Station 7 as a 3-celled chain.

Distribution: Recorded from the European coasts, Atlantic and Pacific America. Mentioned also by Aleem (1950 b) from El-Arish and Port Said.

17. *Grammatophora oceanica* Ehrb.   (Plate II, Figure 6

Cells elongated with frustules appearing slightly swollen at both ends and middle region in valve view; in girdle view septa with a distinct curvature close to the valve edges. Length of cells 50μ, breadth 10μ.

Common, found in May 1956 between Stations 2 and 14 and in February 1956 between Stations 2 and 7.

Distribution: Cosmopolitan; recorded from many parts of the world in the coastal waters.

18. *Grammatophora undulata* Ehrb.   (Plate II Figure 7

Cells rectangular in zigzag chains consisting of 5–7 individuals. Septa prominent and slightly curved. Length 39μ, breadth 30μ. The breadth of the cells in our specimens is considerably larger than in the form described by Hustedt (1931–1937). Valves wavy in girdle view.

Common; found in June and August 1956 at Station 9 and in May 1956 at Station 2.

Distribution: Recorded from the littoral zone of the Mediterranean and other warm-water seas.

19. *Rhabdonema adriaticum* Kütz.   (Plate I Figure 4

Cells quadrangular, adjoined in ribbon-like chains by their valve sides. Due to the shape of the cells the colonies appear almost always in girdle view. Sculpture

of the valves very elaborate and constant. Septa and transapical rows of punctae present at definite intervals. Length of cells 100–120μ, breadth 7–10μ.

Very common. Found in most of the samples collected at the different stations in the Haifa Bay area, especially on rocky bottom. Perennial.

Distribution: This species is a typically littoral form with a world-wide distribution.

20. *Striatella interrupta* Ehrb.   (Plate I Figure 2)

Cells oblong, in valve view lanceolate, with numerous alternate septa reaching almost to the pervalvar margin. Length of cells 40μ. Recorded in chains of 3–5 cells.

Rare, found only in August 1955 between Stations 8 and 9.

Distribution: Known as a littoral form from the Mediterranean and other warm-water seas.

21. *Bacillaria paradoxa* Gmelin

Rectangular elongated cells sliding upon each other. Length 70μ, breadth 4μ.

Common. Found in February 1956 between Stations 2 and 7, in May 1956 between Stations 2 and 14 and in July 1958 at Station 8. A well-known species, euryhaline, known from different water habitats of this country (Rayss 1951; Komarovsky 1953, 1958).

Distribution: Cosmopolitan, euryhaline.

22. *Fragilaria hyalina* (Kütz.) Grunow

Frustules elongated, closely packed together in bundles of four or more cells with parallel margins and rounded ends. Hyaline; transverse striae with very delicate structure. Length 60μ, breadth in girdle view 14–16μ. Chromatophores central, filling a large part of the cell.

Common in Haifa Bay on rocky bottom. Found in large numbers in July 1958 at Station 14.

Distribution: A littoral form frequently found off the European coasts. Recorded also by Aleem (1950 b) from Port Said.

23. *Podocystis adriatica* Kütz.

Cells pear-shaped, with broadly rounded upper end and moderately protracted lower end. Areolated areas between coarse, transverse ribs occur on the valves surface. Length 60–90μ, breadth at upper end 50–55μ, at lower end 12–17μ.

Common, frequently found in April and August 1955, at Stations 8, 9 and 14.

Distribution: Recorded from the Mediterranean and the Atlantic as a common littoral form.

24. *Synedra gaillonii* (Bory) Ehrb. var. *major* n. var.

A typo differt valvis majoribus.

Frustules elongated, slightly inflated in the middle region; margin of valves smooth. Length 300–350μ, breadth at the middle region 25μ, at ends 17–18μ. In the typical form the length is 110–270μ and the breadth 8–11μ (Hustedt 1931–1937).

Common, found in August 1955 between Stations 2 and 7.

Distribution: The type is a littoral species in marine and brackish water habi-tats. Reported also from the Mediterranean (Diannelidis 1950).

25. *Synedra hennedyana* Greg.

Frustules narrow and elongated with pronounced inflation in the middle region and lesser ones at both ends. Length 700–760μ, breadth at the wide region 8–10μ.

> Common in our material. Found in August 1955 between Stations 8 and 9.

Distribution: A littoral species recorded from the Mediterranean Sea and the Atlantic coast of Europe.

26. *Synedra undulata* Bailey

Frustules similar to those of the preceding species except for the undulation of the valves along most of their length. Length 500–600μ, breadth in the middle 15μ, at ends 10μ.

> Common, frequently found on rocky and sandy bottom. Recorded in August 1955 between Stations 8 and 9, February 1956 between Stations 2 and 7, May 1956 between Stations 2 and 14 and in July 1958 at Station 8.

Distribution: A littoral species reported from the Mediterranean and the Atlantic coast of Europe.

27. *Thalassiothrix* frauenfeldii* Grunow

Cells rod-like, linear, united in zigzag or star-like colonies. Ends of cells slightly dissimilar. Length 150–180μ, breadth 3–4μ.

> Rare. Found in May 1956 between Stations 5 and 6.

Distribution: Known from the Mediterranean and the warmer regions of the Atlantic. Sporadically found in the northern regions of that ocean.

28. *Thalassiothrix longissima* Cleve et Grunow

Cells solitary, linear, greatly elongated and slightly curved. Small spines present on the margin of the valves. Length 800μ, breadth 3–5μ.

> Rare. Found in April 1956 between Stations 5 and 6.

Distribution: Cosmopolitan.

29. *Thalassiothrix nitzschioides* Grunow

Cells considerably shorter than in *T. frauenfeldii*, although the colonies have a similar pattern. Length 50μ, breadth 7–8μ.

> Rare, found on *Halimeda tuna* in May 1955 between Stations 7 and 8 and in April 1956 between Stations 14 and Harbour.

Distribution: The species is known from tropical seas and the Mediterranean

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*Species belonging to the genus *Thalassiothrix* are mainly known from the plankton due to their excellent floatability. It is possible, however, that colonies of *Thalassiothrix* species became attached to a submerged surface as might have been in our material, although the possibility that these were frustules which sank to the bottom from the plankton is not excluded.

30. *Anorthoneis excentrica* (Donk.) Grunow

Valves convex, broadly elliptical to almost rounded. Axial area on the valve showing raphe very narrow with elongated central zone, slightly excentrical. Rows of punctae radial. Length 30–40μ, breadth 25–32μ.

Rare, found in April 1955 between Stations 14 and Harbour.

Distribution: Recorded from north European coasts.

31. *Campyloneis grevillei* (W. Sm.) Grunow

Valves dissimilar with rounded ends. Median line not reaching margin in lower valve. Central nodule present. Distinct radial punctae divided into groups by conspicuous radial ribs. Length 45μ, breadth 31μ.

Found in May 1956 between Stations 5 and 7.

Distribution: Reported from Java, the Mediterranean, and the European Atlantic coast-line up to the North Sea.

32. *Cocconeis britannica* Naegeli   (Plate I Figure 5)

Valves broadly elliptical, longitudinal area narrow with central nodule. Double rows of transverse punctae crossed near the valve margin by a longitudinal concentric ring forming characteristic chambers. Valves slightly bent along longitudinal axis. Length 27–54μ, breadth 20–40μ.

A rare species, found only once in May 1956 between Stations 2 and 14.

Distribution: A neritic species reported from the coastal waters of southern Europe.

33. *Achnanthes brevipes* Agardh

Cells narrowly elliptical with a slight constriction in valve view. Valves dissimilar, one with raphe and central nodule, the other with pseudoraphe; bent in girdle view. Length 75μ, breadth 28μ.

Found only as solitary cells in May 1955 between Stations 8 and 9.

Distribution: A cosmopolitan neritic species. This species has previously been reported from a rivulet in Israel south of the Dead Sea (Rayss 1951).

34. *Achnanthes longipes* Agardh

Cells occurring in chains borne on long slender stalks attached to various algae. Valves elongated with a pronounced constriction in valve view and slightly bent in girdle view. Strong ribs and punctae present on the valves. Length 60μ, breadth 26μ.

Found frequently in Haifa Harbour on experimental plates for antifouling paints (Komarovsky and Schwarz 1957, 1959).

Distribution: A cosmopolitan neritic species.

35. *Nitzschia sigma* Kütz.

Frustules slightly swollen in the central region, elongated, with sigmoid ends in girdle view. Length 60μ, breadth in the central region 4μ.

Found only once in July 1958 at Station 8.

Distribution: Common in brackish water ponds (Rayss 1951; Komarovsky 1953)

and coastal waters (Hustedt 1931–1937). Recorded by Aleem (1950 b) from the eastern Mediterranean at El Arish.

36. *Diploneis bombus* Ehrb.
Valves deeply constricted in the middle with almost round upper and lower ends. Length 100μ; breadth 50μ, at constriction level 25μ.

> Rare, found in Haifa Bay in July 1958 at Station 8.

Distribution: Reported by Hustedt (1931–1937) as a cosmopolitan littoral species. Recorded by Zanon (1948) from the coast of Sardinia.

37. *Diploneis crabro* Ehrb.   (Plate II Figure 10)
A very variable species comprising many varieties and forms. Due to the unusually wide range of intraspecific variability, no attempt has been made to determine the exact variety, although the general shape and dimensions of our species correspond well to one of Hustedt's drawings (1931–1937, p. 621, lower right) ascribed by that author to *D. crabro* var. *pandura* (Bréb.) Cleve. Length 36μ, breadth at constriction level 9–10μ, at the expanded region 15–16μ.

> Found in May 1956 between Station 5 and 6.

38. *Diploneis fusca* (Greg.) Cleve var. *aestiva* (Donk.) Hustedt
Valves elliptical with rounded ends and almost parallel sides. Transapical ribs not reaching the median line, exposing a central region, which is almost rectangular in shape. Length 63μ, breadth 35μ.

> Rare, found in Haifa Bay in July 1958 at Station 14.

Distribution: Common in coastal regions of the Mediterranean Sea and in Atlantic.

39. *Diploneis incurvata* (Greg.) Cleve
Cells elliptical with slight constriction in the middle and moderately acuminate ends. Length 56–60μ, breadth 15μ, at constriction level 11–12μ.

> Common, found in Haifa Bay in July 1958 at Station 14.

Distribution: Reported from the Atlantic and the Mediterranean.

40. *Diploneis smithi* (Bréb). Cleve
Valves elliptical with rounded ends; central nodule variable in size and terminal nodule close to the margin. Transapical ribs and horns in central area robust. Length 50–70μ, breadth 20–30μ.

> Found in May 1956 between Stations 2 and 14.

Distribution: A cosmopolitan euryhaline species recorded also from El Arish in the eastern Mediterranean (Aleem 1950 b).

41. *Amphora commutata* Grun.
Cells elongated with slightly convex sides in girdle view; ends truncate. In valve

view dorsal side convex, central side almost straight with ends involuted. Length 107μ, breadth 37μ (in girdle view).

Found in May between Stations 5 and 6.

Distribution: Recorded from the Mediterranean.

42. *Campylodiscus decorus* Bréb.

Valves solitary, saddle shaped, with pseudoraphes at right angles to each other on the two valves. Cells almost circular in valve view with a distinct hyaline area narrowing sharply towards the ends of the cell. Diameter of cells 78–82μ.

Found in May 1956 between Stations 5 and 6.

Distribution: Reported from the Mediterranean, occasionally from the plankton.

CYANOPHYCEAE

CHROOCOCCALES

43. *Chroococcus turgidus* (Kütz.) Naeg.

Usually two-celled with laminated hyaline sheath. Yellowish-green. Diameter of cells 12μ.

Found in July 1955 between Stations 7 and 9.

Distribution: A cosmopolitan euryhaline species found in fresh, brackish and salt water habitats. Recorded from Israel by Frémy and Rayss (1938), Rayss (1944) and Komarovsky (1959).

44. *Synechocystis aquatilis* Sauv.

Cells round, solitary or in groups of 2–3. Pale blue-green; gelatinous sheath indistinct. Diameter of cells 5–6μ.

Found in June 1955 between Stations 7 and 9, in blooming condition.

Distribution: Cosmopolitan. Recorded also from the freshwater plankton of Israel (Rayss 1944; Komarovsky 1951, 1953).

45. *Xenococcus schousboei* Thur.

Colonies almost round, formed of pseudoparenchymatous, closely bound polygonal cells, 3–5μ wide. Diameter of colony 44μ.

Rare, found in July 1958 at Station 14.

Distribution: Found in the Adriatic Sea, northern European and American coasts of the Atlantic.

HORMOGONALES

46. *Calothrix confervicola* (Roth) Agardh

Colonies rosette-shaped with filaments attenuated towards the distal ends and heterocysts at the base of the trichomes. Trichomes 16μ thick at base, up to 1 cm long including the attenuated section. Cells 4–6μ long.

Found in April 1956 at Station 14 as an epiphyte on *Polysiphonia sanguinea*.

Distribution: Cosmopolitan, reported from the western Mediterranean by Feldmann (1937) and from the eastern part by Aleem (1950 a).

47. *Lyngbya aestuarii* (Mert.) Liebmann

Filaments single, almost straight with pronounced colourless sheath and closely packed granulated cells without any constrictions at crosswalls. Apical cell rounded, without a calyptra. Diameter of trichome $10–14\mu$; width of surrounding sheath $5–6\mu$. Length of individual cell $5–6\mu$.

> Very common in the material collected during July 1958 at Station 14. The species is known to be very variable both in dimensions and certain morphological characteristics (Jao 1948).

Distribution: Cosmopolitan. Reported from the Mediterranean by Feldmann (1937).

48. *Lyngbya agardhii* Gom.

Syn.: *Lyngbya livida* Ard.

Trichomes surrounded by gelatinous sheaths enclosing numerous hormogonia. Length of trichomes 2–15 mm, their breadth $5–10\mu$; breadth of the gelatinous sheath 1μ. Cells shorter than wide, about $2–5\mu$ long.

> Found in large numbers in November 1955 between Stations 1 and 14 as an epiphyte on *Laurencia obtusa* and *Crouania attenuata*.

Distribution: Adriatic Sea, Mediterranean, European coasts of the Atlantic; the English Channel; European and American coasts of the Pacific.

49. *Lyngbya confervoides* C. Agardh

Filaments entangled and attached to the substrate by their base. Trichomes 24μ wide and 1 cm long. Hyaline sheaths $3–4\mu$, not staining with chlor-zinc-iodide. Cells considerably shorter than wide, $3–4\mu$ long. Septa granulated, apical cell rounded, calyptra absent.

> Found in September 1956 at Station 14 as an epiphyte on *Halimeda tuna*.

Distribution: Cosmopolitan, recorded from the western Mediterranean (Feldmann 1937) and from the eastern parts (Aleem 1950 a).

50. *Oscillatoria limosa* Ag.

A very variable species. Trichomes $11–12\mu$ wide. Cells much wider than long, not constricted at the cross walls.

> Found in May 1956 between Stations 5 and 6.

Distribution: Cosmopolitan; euryhaline.

51. *Oscillatoria margaritifera* Kütz.

Trichomes yellowish blue, slightly bent, constricted at cross walls. Cells 24μ broad, $5–6\mu$ long, granulated along cross walls. End-cell convex with a very narrow calyptra.

> Found in May 1956 between Stations 7 and 8.

Distribution: Cosmopolitan, in saline waters. Reported from the Mediterranean (Feldmann 1937; Aleem 1950 a) and from the Red Sea (Rayss 1959).

52. *Oscillatoria nigro-viridis* Thwaites in Harvey

Trichomes olive green, slightly constricted at cross walls, tapering at the end. Cells 7μ broad, 4μ long, granulated at cross walls.

Found in May 1955 between Stations 7 and 8.

Distribution: Probably cosmopolitan. Recorded from the Mediterranean by Feldmann (1937) and Aleem (1950 a).

53. *Spirulina subsalsa* Oerst.

Turns of the spiral close together; yellow-green. Length 330μ, breadth 4μ.

Found in July 1958 between Stations 5 and 6.

Distribution: Common in standing brackish water and in marine environments. Cosmopolitan. Reported also from the Mediterranean (Feldmann 1937).

DISCUSSION

In the present work 42 species of diatoms and 11 species of blue-green algae were recorded.

As mentioned above, a large part of the microscopic algae was lost in the course of the preliminary treatment of the material on board the vessel. The data outlined here, therefore, give only a first indication of the very rich and varied flora occurring in the particular habitat under consideration. Moreover, a considerable number of naviculoid diatoms which occurred in the samples were omitted from the foregoing description; due to the lack of pertinent literature relating to this group, no attempt was made to describe and identify the species.

A close examination of the distribution of the species described in this report shows both definite zonation according to depth and differences according to types of sea bottom. As can be seen in Map 1, the stations selected for the collection of the samples cover all the depths in the Haifa Bay area from 10 fathoms in the most shallow region to about 50 fathoms at the greatest depth. Most of the diatom species were found at depths of 10–25 fa., where the sea bottom consists mostly of fine sand and scattered rocks. At greater depths on mud flats only five diatom species were found, of which at least three are known from the plankton. The small number of species recorded from the mud flats, however, is not significant, as this type of sea bottom does not constitute a suitable substrate for the attachment of macroscopic algae. It is, therefore, possible that if the superficial layers of this mud bottom were examined for the presence of microscopic algae, the results would have been quite different. Hustedt and Aleem (1951), for example, found some 132 species of diatoms on the mud flats of Salstone near Plymouth.

Out of a total of 42 species of diatoms, only 10 belong to the Centricae; of the latter, at least half are truly planktonic and their presence on deep water algae

can be attributed to their sinking to the bottom. As the material was examined only after preservation in formaldehyde, it is difficult to ascertain whether these cells were in a living state or not after reaching the sea bottom.

The origin of this benthonic community of microscopic algae is threefold. Some of the species, mainly the colonial forms, which are usually attached to the macroscopic algae by a thin stalk, probably originate from the rocky shore. Such species as *Rhabdonema adriaticum*, *Licmophora ehrenbergii*, *L. flabellata*, *Grammatophora oceanica* and *G. undulata* belong to this category. Other species, mainly
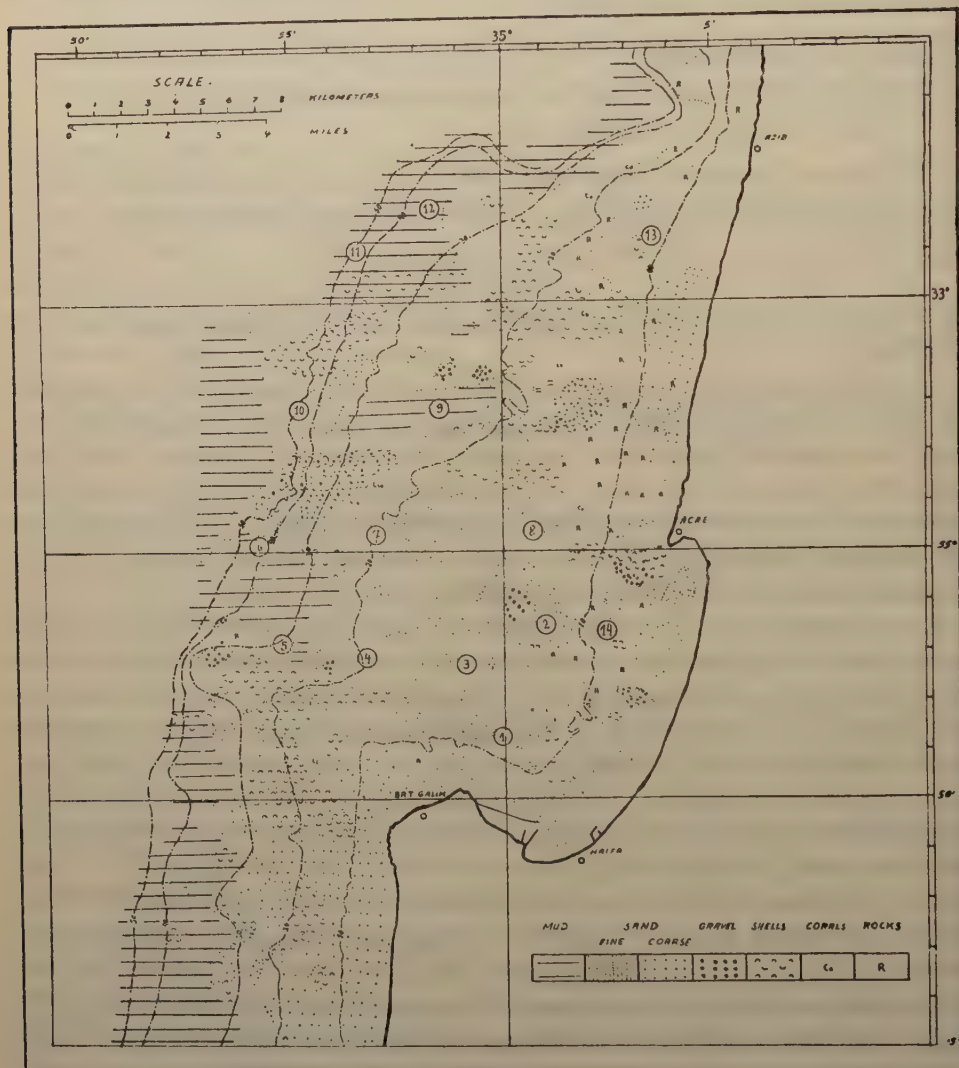
Map 1
Haifa Bay showing location of stations and types of sea bottom.

centric diatoms like *Coscinodiscus radiatus*, *C. excentricus* and *Triceratium favus* are definitely planktonic. A number of species considered as euryhaline may have reached the Haifa Bay region through the Kishon River flowing into it. Such species comprise *Bacillaria paradoxa* and *Nitzschia sigma* among the Diatomeae and *Chroococcus turgidus* and *Synechocystis aquatilis* among the Cyanophyceae.

Regarding the distribution of Cyanophyceae, representatives of both Hormo-gonales and Chroococcales were recorded.

Most of the species were found in shallow water at 10–12 fa. depth.

The details regarding the seasonal distribution of individual species are given in the above description. No attempt, however, has been made to draw any general conclusions in this respect, as the authors feel that the number of samples examined and the frequency of the collections are not sufficiently comprehensive.

This report is, therefore, to be regarded as a preliminary attempt to throw light on a relatively little known community which may have an important role in the general metabolism of the sea.

REFERENCES

ALEEM, A. A., 1950a, Some Cyanophyceae from the eastern Mediterranean, *Contr. from the mar. bot. Inst. Göteborg*, No. **6**, 303–307.

ALEEM, A. A., 1950b, Littoral diatoms from the eastern Mediterranean, *Contr. from the mar. bot. Inst. Göteborg*, No. **7**, 309–325.

ALLEN, W. E. AND CUPP, E. E., Plankton diatoms of the Java sea, *Ann. Jard. bot. Buitenz.*, **44**, 101–174.

BODEN, B. P., 1950, Some marine plankton diatoms from the West Coast of South Africa, *Trans. roy. Soc. of S. Afr.*, **32**(4), 321–434.

DIANNELIDIS, T., 1950, Contribution à la connaissance des algues marines des Sporades du Nord. II. Bacillariophyta, *Praktika of the Hell. hydrob. Inst.* Athens, 4(1),35–50.

EDELSTEIN, T., Contribution to the knowledge of the benthonic algae of Haifa Bay. Systematics and ecology (in preparation).

FELDMANN, J., 1937, Les algues marines de la Côte des Albères, I–III. Cyanophyceés, Phaeophycées, *Rev. algol.*, **9**, 1–197.

FELDMANN, J., 1938, Recherches sur la végétation marine de la Mediterranée, *Rev. algol.*, **10**, 1–345.

FELDMANN, J., 1959, Les cyanophycées marines de la Guadeloupe, *Rev. algol.* (n.s.), **4** (1), 25–40.

FREMY, P. ET RAYSS, T., 1938, Algues des sources thérmales de Kallirrhoë (Transjordanie), *Palest. J. Bot. Jerusalem*, **1**, 27–37.

GEITLER, L., 1932, Cyanophyceae, In *Rabenhorst's Kryptogamenflora*, **14**, 1–1195, Leipzig.

GHAZZAWI, F. M., 1933, The littoral diatoms of Liverpool and Port Erin shores, *J. mar. biol. Ass.* Plymouth, **19**, 165–176.

GHAZZAWI, F. M., 1939, A study of the Suez Canal plankton, *Hydrob. and Fish. Direct. Notes and Memoires*, Cairo, *No.* **24**, 1–83.

GOTTLIEB, E., 1959, A study of the benthos in Haifa Bay. Ecology and zoogeography of the inverte-brates. Ph. D. Thesis, The Hebrew University of Jerusalem, 1–131 (Mimeographed; in Hebrew with English abstract).

HUSTEDT, F., 1927–1930, Die Kieselalgen, in *Rabenhorst's Kryptogamenflora*, **7**, *I*, Centricae, 1–920, Leipzig.

HUSTEDT, F., 1931–1937, *II*, Pennatae, 1–736, *Ibid.*, Leipzig.

HUSTEDT, F., 1955, Marine littoral diatoms of Beaufort, North Carolina, *Duke Univ. mar. Stat.* Durham, North Carolina, *Bull. No.* **6**, 1–67.

HUSTEDT, F. AND ALEEM, A. A., 1951, Littoral diatoms from the Salstone, near Plymouth, *J. mar. biol. Ass.*, Plymouth, **30**, 177–196.

IOANNOU, M. M., 1949, Note sur *Bellerochea malleus* (Brightwell) van Heurck, *Praktika of the Hell. hydrob. Inst.* Athens, **4**, (1), 33–38.

JAO, C. C., 1948, The marine Myxophyceae in the vicinity of Friday Harbour, Washington, Repr. *Bot. Bull. of Acad. Sin.*, **2**, 161–177.

KOMAROVSKY, B., 1951, Some characteristic water-blooms in Lake Tiberias and fish ponds in the Jordan Valley, *Int. Ass. theor. and appl. Limnol.*, **11**, 219–223.

KOMAROVSKY, B., 1953, A comparative examination of the phytoplankton of several fish ponds in relation to some of the essential chemical constituents of the water, *Sea Fish. Res. Stat.* Cae-sarea (now in Haifa), *Bull. No.* **5**, 379–410.

KOMAROVSKY, B., 1958, Contribution to the knowledge of Lake Huleh, *Fish. Bull.* Haifa, *No.* **15**, 20–26 (In Hebrew with English abstract).

KOMAROVSKY, B., 1959, The plankton of Lake Tiberias, *Sea Fish. Res. Stat.* Haifa, *Bull. No.* **25**, 65–96.

KOMAROVSKY, B. AND SCHWARZ, L., 1957, A study of marine antifouling paints in Israel, *Gen. Fish. Council Med. Proc.*, *FAO*, Rome, *techn. Pap.*, **4**, 347–361.

KOMAROVSKY, B. AND SCHWARZ, L., 1959, The behaviour of marine antifouling paints in the Kishon Harbour, *Gen. Fish. Council Med. Proc. FAO*, Rome, *techn. Pap. No.* **57**, 1–6.

LEBOUR, M., 1930, The planktonic diatoms of northern seas, *Roy Soc.*, London, **116**, 1–244.

PAVILLARD, J., 1925, Bacillariales, *Rep. Dan. ocean. Exp.* 1908–10 *to the Med. and adj. Seas*, **2**, *Biol.*, 1–72.

POLITIS, J., 1949, Diatomées marines de Bosphore et des îles de la mer de Marmara, *Praktika of the Hell. hydrob. Inst.*, Athens **4**, (1), 11–30.

RAYSS, T., 1944, Matériaux pour la flore algologique de la Palestine. I. Les Cyanophycées, *Palest. J. Bot. Jerusalem*, **3**, 94–113.

RAYSS, T., 1951, Matériaux pour la flore algologique de la Palestine. II. Les algues des eaux con-tinentales, *Palest. J. Bot. Jerusalem*, **5**, 71–95.

RAYSS, T., 1959, Contribution à la connaissance de la flore marine de la Mer Rouge, *Sea Fish. Res. Stat.* Haifa, *Bull. No.* **23**, 1–32.

ZANON, V., 1940, Diatomee de Rovigno, *Thalassia*, **3**, (9), 1–72, Venice.

ZANON, V., 1947, Diatomee de la Isole Ponziane. Materiale per una florula diatomologica del mare Tirreno, *Boll. di Pesca, Pisc. e Idrob.* Rome, (n. s.), **2**, 36–53.

ZANON, V., 1948, Diatomee marine di Sardegna e pugillo di alghe marine della stessa, *Boll. di Pesca, Pisc. e Idrob.* Rome, (n. s.) **3**, 202–256.

CHANGES IN THE CONTENT OF GERMINATION REGULATING SUBSTANCES IN LETTUCE SEEDS DURING IMBIBITION

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ABSTRACT

Lettuce seeds of the variety Grand Rapids were investigated for their content of germination regulating substances. The dry seeds were shown to contain only germination inhibitors but during germination these inhibitors disappeared and other germination inhibitors and germination stimulators appeared. Thiourea and coumarin were shown to affect the pattern of germination regulating substances during germination.

INTRODUCTION

Some varieties of lettuce seed are known to require light for their germination while others are indifferent to light. The light requirement of the variety Grand Rapids is abolished if the seeds are germinated at low temperatures (Evenari 1949), it is also abolished at higher temperatures if the seeds are treated with thiourea (Thompson and Kosar 1939). On the other hand, light-indifferent varieties (e.g. Progress) may be converted into light-requiring varieties, if treated with coumarin (Nutile 1945). Coumarin is a naturally-occurring growth inhibitor, and Neumann (1959) has suggested that it should be regarded as an auxin. Thiourea is known as a dormancy-breaking substance not only in the case of the seeds referred to, but also in tubers and buds (Denny, Miller and Guthrie 1930). It is known that bud and tuber dormancy is in some way connected with plant hormones (Samish 1954, Bently 1958). It seemed possible, therefore, that the light requirements of lettuce seeds might also be linked with hormone metabolism. This view was supported by the findings of Poljakoff-Mayber (1958) and Poljakoff-Mayber, Mayer and Zacks (1959) who showed that the germination of lettuce seeds var. Grand Rapids was stimulated by IAA. The treatment was more effective the deeper was the dormancy of the seeds or the lower the temperature during germination. Another attempt was made (Poljakoff-Mayber, Blumenthal-Goldschmidt and Evenari 1957) to correlate the ability of the seeds to germinate with the plant growth substances they contain. It was shown that dry seeds do contain growth inhibiting substances which disappear during germination. But there is no evidence whatsoever that the inhibitory activity of these substances in conventional extension growth tests reflects the

effect of these substances on the germination process. A test was therefore devised which enables us to study the effect of the growth active substances on germination (Blumenthal-Goldschmidt 1958a). The present paper summarizes the results of a investigation into the germination inhibiting or promoting substances occurring naturally in lettuce seeds, and the changes in these substances which take place during germination, both in the presence and absence of the stimulator thiourea or the inhibitor coumarin.

MATERIAL AND METHODS

Lettuce seeds (*Lactuca sativa* L.) var. Grand Rapids, supplied by Ferry Morse U.S.A., were used for the experiments. 25 g of seeds were sown in Petri dishes, in water or a solution of either coumarin (100 mg/l) or thiourea (1250 mg/l). The dishes were kept in the dark for 2 to 12 hours at 26°C. The seeds or seedlings were then harvested, dropped into boiling ethanol, ground and extracted with absolute ethanol as described previously (Blumenthal-Goldschmidt 1958a).

12.5 mg coumarin or 1 mg thiourea extracted in the same manner were used as controls. The second etheric extracts were separated by paper chromatography. The chromatograms were tested on germination of lettuce seeds as previously described (Blumenthal-Goldschmidt 1958a).

RESULTS

The germination-regulating substances which were detected in dry seeds and in seeds which had been imbibed for 2 to 12 hours are shown in Figure 1.

As is evident from this figure, the acid fractions of extracts of dry lettuce seeds reveal an inhibitory zone at Rf 0.25–0.55, while the neutral fraction shows two inhibitory zones at Rf 0.15 and 0.55–0.9 respectively. On imbibition in water, the acid inhibitor present in the dry seeds disappears. This occurs in stages: After two hours imbibition the central part of the zone disappeared; after 4 hours the greater part is no longer detectable, and after 12 hours of imbibition, when the radicle actually starts to produce, the seeds do not contain any acid germination inhibitor. During imbibition, however, another inhibitor (Rf 0.8) appears, and disappears again after 12 hours.

In the neutral fraction, the low Rf inhibitor apparently decreases in amount during the initial phases of imbibition, but increases again just before the protrusion of the radicle becomes detectable, after about 12 hours imbibition. The higher Rf zone seems to contain several substances, which may be divided into three groups. The middle group disappears during imbibition, while the lower and the higher groups remain in the seeds throughout the imbibition period. In the histogram of the seeds imbibed for 12 hours the Rf's of these two groups seem to be lower than in the other histograms, and they might possibly be considered as new substances. More probably, however, the lower Rf may be explained by the changed composition
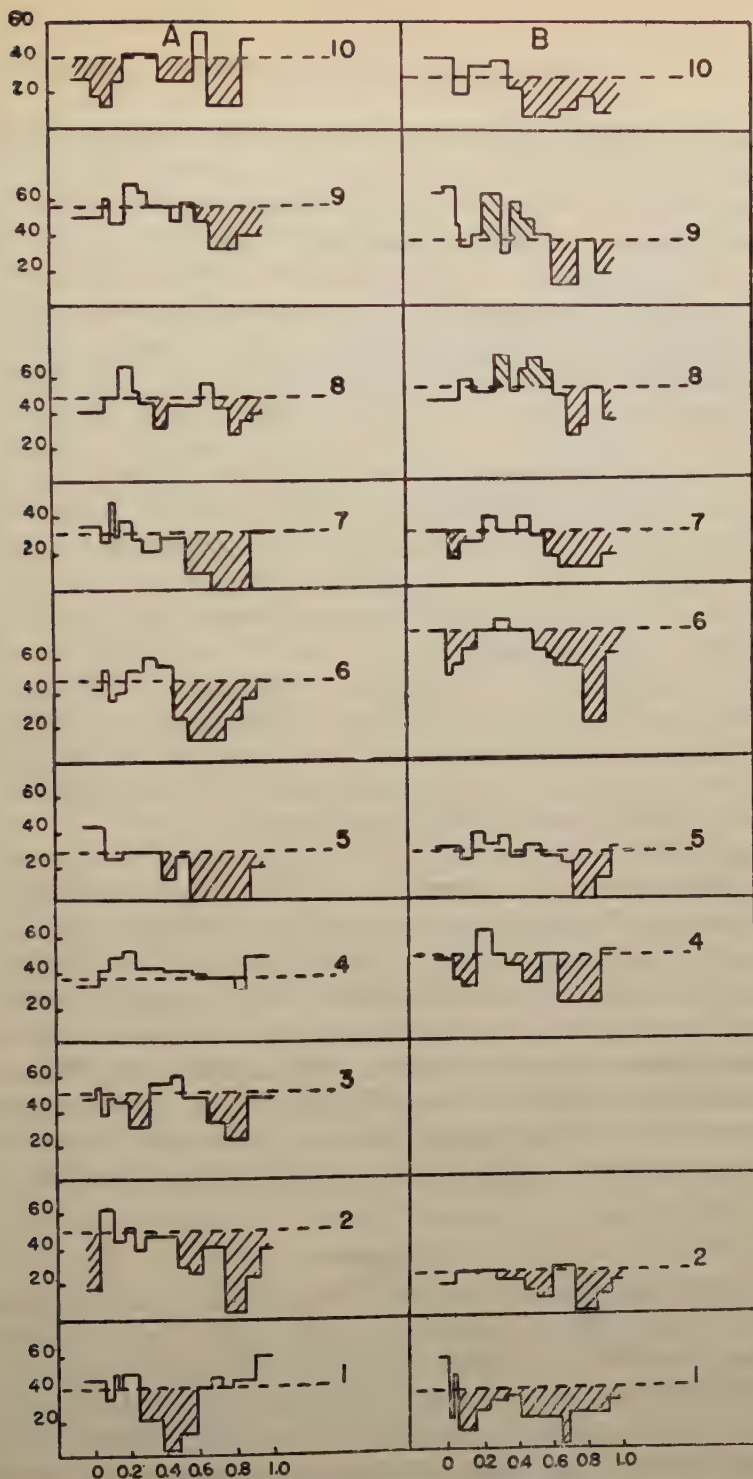
Figure 1

Histograms showing the chromatographic separation of germination active substances extracted from lettuce seeds imbibed for various lengths of time. The substances were assayed by their effect on the germination of lettuce seeds. A—Acid fraction of extracts. B—Neutral fraction of extracts. 1—Dry seeds, 2—Two hours imbibition in water, 3–Four hours imbibition in water, 4—Twelve hours germination in water, 5—Coumarin control, 6—Two hours imbibition in coumarin, 7—Twelve hours imbibition coumarin, 8—Thiourea control, 9—Two hours imbibition in thiourea, 10—Twelve hours germination in thiourea. The broken line gives the germination of lettuce seeds in water.

of the extracts which may contain a higher concentration of substances which slow down the Rf's.

Parallel investigations were carried out with seeds imbibed with coumarin or thiourea (See Figure 1). Coumarin appears to give rise to derivatives during the extraction procedure, since the pure substance, run directly, gives a fluorescent inhibitory zone at Rf 0.90 whereas if it is subjected to the extraction procedure the active zone in the acid extract is 0.60–0.85. Chromatograms of seeds imbibed in coumarin show the same wide zone of inhibition, i.e. 0.60–0.85. This zone also covers the area of the natural acid inhibitors (Rf 0.8) which appear during imbibition in water. This zone is present in all extracts of imbibed seeds, in water, coumarin or thiourea, and there are indications that it may also be present in dry seeds. The acid fraction of the seeds imbibed in thiourea for two hours does not differ from the same fraction of water imbibed seeds. After 12 hours, however, the thiourea imbibed seeds contain many more germination-inhibitory substances than do the water imbibed seeds, although the latter germinate to the extent of 30 per cent, while the thiourea imbibed seeds germinate to 100 per cent. The chromatogram of the acid fraction derived from pure thiourea subjected to the extraction procedure does not show any definite zone promoting germination except for some slight effect in Rf 0.2. The lack of clear germination stimulation may be due to the fact that the thiourea as a result of its slight basic properties forms salts in the acidified extracts and remains in the water fraction (see also Luckwill 1957).

When pure coumarin is subjected to the extraction procedure, the neutral fraction shows inhibitory activity at about Rf 0.80 (Figure 1B). This inhibitory zone also appears in extracts of coumarin imbibed seeds. It also coincides with the inhibitor present in water—and possibly thiourea—imbibed seeds. The slow running neutral inhibitor (Rf 0.15) formed in he seeds imbibed in water appears in the coumarin imbibed seeds as well, but its existence in those imbibed in thiourea is doubtful.

The neutral fraction made from thiourea imbibed seeds shows definite germination-promoting activity after two hours imbibition, but these promoting substances disappear again when visible germination begins (12 hours imbibition). These are the only clear-cut promotors of germination detected in this investigation.

DISCUSSION

This investigation has shown that dry lettuce seeds contain several germination inhibitors which change or disappear during the imbibition and germination processes. No germination promoting substances have been detected in dry seeds. During imb.bition in water, part of the inhibitory substance is lost. During imbibition in coumarin, the latter appears to be taken up by the seeds. Extracts of such seeds contain large amounts of germination inhibiting substances, not all of which seem to be coumarin itself. The uptake of coumarin by lettuce seeds was demonstrated by Mayer (1953), who also showed that coumarin is destroyed or metabolized by

seed extracts. The coumarin may therefore be converted by the seeds to coumarin derivatives, some of which may be germination inhibitors. Analysis of extracts of seeds imbibed in the germination stimulator — thiourea — shows that such seeds still contain at least part of their natural inhibitory substances, but promoting substances are also present.

The inhibitory substances found in the neutral fraction of extracts of dry and water-imbibed seeds are of approximately the same Rf as those found in extracts of seeds imbibed in coumarin, but differ somewhat in Rf from those found in seeds imbibed in thiourea.

Several attempts have been made to explain dormancy and its breaking by changes in the naturally-occurring promoting and inhibitory substances. The most widely known of these attempts are those of Hemberg (1949, 1954, 1958) and Szalai (1959) to explain the rest period of potato tubers, and those of Hemberg (1955a, b), Lasheen et al. (1956), Biggs (1959), Galitz et al. (1959), Linser et al. (1958) and Cartright et al. (1955), to explain seed dormancy and its breaking. Most of the substances isolated in those investigations were assayed by means of conventional tests for auxins and not by means of tests related to the phenomenon under study. When an attempt was made to use such a related test, it was found that the earlier explanation lost its validity (Buch and Smith 1959). Other authors (Cartright, Sykes and Wain 1955) doubted the explanation from the beginning and attributed to the identified hormones only some role in regulating the growth of the seedling or the embryo. In the results presented in this paper a correlation may be found between the presence of certain germination inhibitors and the germination of the seeds in water. The presence of all these inhibitors, especially in the neutral fraction, may explain the low germination of lettuce seeds (var. G.R.) in the dark.

It would be interesting to compare the extracts of seeds germinating in the dark with those of seeds germinating after illumination. As is shown elsewhere (Blumenthal-Goldschmidt 1958b), there are present, in the dark-imbibed seeds, substances which also strongly inhibit root and shoot extension growth.

The dry and water-imbibed seeds contain germination inhibitors similar in Rf to those which are observed in much larger amounts in coumarin-treated seeds, and which may be closely related to coumarin. It is possible that when seeds are germinated in water these substances must first be broken down by metabolism before embryo growth can proceed. When on the other hand, seeds are germinated in coumarin, the addition of further inhibitory coumarin derivatives to those already native in the seed results in an accumulation greater than can be destroyed during metabolism, and germination is blocked.

Imbibition in thiourea brings about the formation and accumulation of germination-stimulating substances and they may change the equilibrium towards processes favouring germination.

A similar equilibrium between growth inhibitors and a germination stimulator has been reported for *Fraxinus* seeds (Villiers and Wareing 1960).

While it has been thus possible to correlate much of the observed germination behaviour of the seeds with their content of inhibitors and stimulators, it does not seem likely that this is the only mechanism involved in regulating the various dormancy phenomena. It is possible that the stimulators and inhibitors function in conjunction with some other factor as yet unknown.

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REFERENCES

BENTLY, J. 1958, The naturally-occurring auxins and inhibitors, *Annual Rev. Plant Physiol.*, **9**, 47.

BIGGS, R. H., 1959, Relation of growth substances to after-ripening of peach seeds, *Plant Physiol.*, **34**, Suppl. p. 7.

BLUMENTHALGOLDSCHMIDT, S., 1958a, Some further investigations on the growth active substances extractable from dry lettuce seeds, *Bull. Res. Counc. of Israel*, **6D**, 91.

BLUMENTHAL-GOLDSCHMIDT, S., 1958b, Plant growth substances in germinating lettuce seeds, Ph.D. Thesis, The Hebrew University of Jerusalem (in Hebrew).

BUCH, M. L. AND SMITH, O., 1959, The acidic growth inhibitor of potato tuber in relation to their dormancy, *Physiol. Plant.*, **12**, 706.

CARTRIGHT, P. M., SYKES, J. T. AND WAIN, R. L., 1955, The distribution of natural hormones in germinating seeds and seedling plants. The chemistry and mode of action of plant growth substances, *Proceed. Symp. Wye College*, p. 32, Butterworth's Scientific Publications, London.

DENNY, F. E., MILLER, L. D. AND GUTHRIE, J. D., 1930, Enzyme activities of juices from potatoes treated with chemicals that break the rest period, *Cont. Boyce Thompson Inst.*, **2**, 417.

EVENARI, M., 1949, Germination inhibitors, *Bot. Rev.*, **15**, 153.

GALIZ, D. S. AND HOWELL, R. W., 1959, The occurrence and physiological properties of a natural inhibitor of germination in immature soya bean seeds, *Plant Physiol.*, **34**, Suppl. p. 10.

HEMBERG, T., 1949, Significance of growth-inhibiting substances and auxins for the rest-period of the potato tuber, *Physiol. Plant.*, **1**, 24.

HEMBERG, T., 1954, Study on the occurrence of free and bound auxins and of growth inhibiting substances in the potato tuber, *Physiol. Plant.*, **7**, 212.

HEMBERG, T., 1955a, Studies on the balance between free and bound auxin in germinating maize, *Physiol. Plant.*, **8**, 2.

HEMBERG, T., 1955b, The auxin balance during germination in untreated maize kernels and in maize kernels treated with IAA, *Svensk bot. Tidskr.*, **48**, 4.

HEMBERG, T., 1958, The significance of the inhibitor β complex in the rest period of the potato tuber, *Physiol. Plant.*, **11**, 615.

LASHEEN, A. M. AND BLACKHURT, H. T., 1956, Biochemical changes associated with dormancy and after-ripening of blackberry seed, *Proceed. Amer. Soc. hort. Sci.*, **67**, 331.

LINSER, H., KIERMAYER, O. AND JONSSEF, E., 1958, Der Wuchsstoffgehalt verschiedener *Brassica*-flanzen in Abhängigkeit von ihrem Entwicklungszustand, *Planta*, **52**, 173.

LUCKWILL, L. C., 1957, Studies of fruit development in relation to plant hormones, *J. hort. Sci.* **32**, 18.

MAYER, A. M., 1953, Quantitative aspects of the behaviour of coumarin as a germination inhibitor, *Physiol. Plant.*, **6**, 413.

MIMAULT, J., 1956, Mise en evidence et variations d'activité d'auxines et de substances inhibitrices de croissance dans les extraits de graines de quelques variétés de fruits, *J. Recherches C.N.R.S.*, **37**.

NEUMANN, J., 1959, An auxin-like action of coumarin, *Science*, **129**, 1675.

NUTILE, G. E., 1945, Inducing dormancy in lettuce seeds with coumarin, *Plant Physiol.*, **20**, 433.

POLJAKOFF-MAYBER, A., 1958, The effect of auxin and anti-auxin on germination of lettuce seeds, *Bull. Res. Counc. of Israel*, **6D**, 78.

POLJAKOFF-MAYBER, A., BLUMENTHAL-GOLDSCHMIDT, S. AND EVENARI, M., 1957, The growth substances content of germinating lettuce seeds, *Physiol. Plant.*, **10**, 14.

POLJAKOFF-MAYBER, A., MAYER, A. M. AND ZACKS, S., 1958, Interaction in growth and germination between thiourea and indolyl acetic acid, *Ann. Bot., Lond.*, **22**, 175.

SAMISH, R. M., 1954, Dormancy in woody plants, *Annual Rev. Plant Physiol.*, **5**, 183.

SZALAI, I., 1959, Quantitative changes of growth-promoting and inhibiting substances in the potato tubers treated with rindite, *Physiol. Plant.*, **12**, 237.

THOMPSON, R. C. AND KOSAR, W. F., 1939, Germination stimulation of dormant lettuce seeds by sulfur compounds, *Plant Physiol.*, **14**, 567.

VILLIERS, T. A. AND WAREING, P. F., 1960, Interaction of growth inhibitor and natural germination stimulator in the dormancy of *Fraxinus excelsior* L., *Nature*, **185**, 112.